

¹ Satellite-detected droughts predict plant life history

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Abstract

12 Explaining variation in life history strategies is a long-standing goal of evolutionary biology.
13 For plants, annual and perennial life histories are thought to reflect adaptation to
14 environments that differ in the frequency of environmental stress such as drought. Here we
15 test this hypothesis in *Heliophila* (Brassicaceae), a diverse genus of flowering plants native to
16 Africa by integrating 2192 herbaria occurrence records with 34 years of satellite-based
17 drought detection. Consistent with predictions from classic life history theory, we find that
18 perennial *Heliophila* species occur in environments where droughts are significantly less
19 frequent compared to annuals. These associations are predictive while controlling for
20 phylogeny, lending support to the hypothesis that drought related natural selection has
21 influenced the distributions of these strategies. Additionally, the difference in drought
22 frequency between annual and perennial species distributions is greatest during the summer
23 and fall, which also appears to be when annuals are in the seed phase of their life cycle based
24 on collection dates of annual species. Together, these finding provide empirical support for
25 classic hypotheses about the drivers of life history strategy in plants - that perennials out
26 compete annuals in environments with less frequent drought and that annuals are adpated to
27 enviroments with more frequent drought by escaping drought prone seasons as seeds.

28

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

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31 **Introduction**

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

44 Classical theory predict shorter life spans in environments where adult mortality is
45 high (Charnov & Schaffer, 1973; Franco & Silvertown, 1996; Stearns, 1992). In plants, this
46 has been extended to the hypothesis that annuality is adaptive when it allows plants to
47 escape drought (Schaffer & M, 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 & D'Antonio, 2004). These predictions
54 have been supported by the association of annuality with arid environments in wild rice
55 (Morishima, Sano, & Oka, 1984) and *Oenothera* (Evans, Hearn, Hahn, Spangle, & Venable,

56 2005). Additionally, annual and perennial species of *Nemesia* were qualitatively associated
57 with winter rather and summer rainfall environments respectively (Datson, Murray, &
58 Steiner, 2008) and annual species of *Scorzoneroidea* were associated with environments
59 classified as unpredictable (Cruz-Mazo, Buide, Samuel, & Narbona, 2009). However, whether
60 the history frequency of drought events indeed predicts the distributions annual or perennial
61 life history strategies has yet to be tested in a phylogenetic context with suitable sample
62 sizes of distribution and climate data.

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

75 Materials and Methods

76 Data

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

79 **Satellite-detected drought data.** Remotely sensed data is a powerful tool for
 80 characterizing seasonal patterns in drought because it is less limited in spatial and temporal
 81 scope and resolution than weather stations or field observations (AghaKouchak et al., 2015).
 82 To quantify the frequency of drought during different seasons across landscapes, we used the
 83 remotely sensed Vegetative Health Index (VHI), which measures landscape scale reductions
 84 in plant cover and temperature conditions characteristic of drought (Kogan, 2001).
 85 Generated from data collected by NOAA AVHRR satellites since 1981, the VHI combines
 86 normalized difference vegetation index (NDVI) derived measures of vegetative stress
 87 (Vegetative Condition Index - VCI) with temperature stress indicated by anomalies in
 88 thermal spectra (Temperature Condition Index - TCI). The VHI of year y during week w of
 89 [1, 52] at pixel i is derived from the following equations, where n is the number of years
 90 observed.

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

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

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

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

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

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

94 Thus, VHI measurements are standardized according to conditions historically observed at
 95 each locations. These measurements have been validated and generally used for evaluating
 96 drought risk and predicting crop yields in agriculture (e.g., Rojas, Vrieling, & Rembold, 2011;

97 Kogan et al., 2016). But they also present a new tool to study seasonal patterns in the
98 frequency of drought across environments and to test hypotheses about the effect of drought
99 on ecological and evolutionary processes (Kerr & Ostrovsky, 2003). As such, the VHI has
100 been applied recently to study drought related ecology of natural species and proven useful
101 for predicting infraspecific variation in drought tolerance traits and genes (Dittberner et al.,
102 2018; Mojica et al., 2016; Monroe et al., 2018). Here, we accessed VHI data at 16km²
103 resolution from 1981 to 2015
104 (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) to characterize the
105 seasonal drought frequencies experienced by annual and perennial *Heliophila* species.

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

Heliophila occurrence records. Botanists have collected and maintained over 350 million botanical specimens worldwide over the past 300 years. Herbarium specimens and their associated metadata have been used since the 1960s to study species' geographical distributions (reviewed by Willis et al. (2017) and Lang, Willems, Scheepens, Burbano, and Bossdorf (2018)). And as they become digitized (Soltis, 2017), these collections have been used to study relationships between trait distributions, geography, and climate (Davis, Willis, Connolly, Kelly, & Ellison, 2015; Stropp et al., 2016; Václavík, Beckmann, Cord, & Bindewald, 2017; Wolf, Zimmerman, Anderegg, Busby, & Christensen, 2016). To characterize the diributions of annual and perennial *Heliophila* species, all records for the genus *Heliophila* were downloaded from the Global Biodiversity Information Facility (gbif.org) on July 21, 2018 (“GBIF occurrence download,” 2018).

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

Analyses

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

145 **Filtering of occurrence records.** To avoid instances with spurious location data,

146 we filtered raw GBIF by restricting our analyses to include only:

- 147 • Records for species with reported life history
- 148 • Records with geospatial data
- 149 • Records without known geospatial issues (i.e., coordinates reported are those of
150 herbarium)
- 151 • Records from collection sites classified as land pixels
- 152 • Records from Africa
- 153 • Records without duplicates (i.e., identical species, location, collection date)

154 **Phylogeny construction.** Out group species were aligned together with *Helophilus*

155 ITS sequences using MAFFT. Model selection for construction of phylogeny was performed

156 in jModeltest2 with CIPRES. Based on this analysis, *GTR + L* were selected. Ultrametric

157 phylogeny was estimated with branch lengths as relative time.

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

159 To evaluate the hypothesis that annual and perennial life history strategies reflect
160 adaptations to alternative drought regimes, we tested the corresponding prediction that the
161 observed distributions of annual and perennial *Helophilus* species would be significantly
162 associated with historic drought frequency. First, we compared the frequency of drought
163 during the winter, spring, summer, and fall between raw occurrence records of annual and
164 perennial species by t-tests. To account for variation in the number of occurrence records per
165 species, we next calculated the mean drought frequency during the winter, spring, summer
166 and fall for each species. The relationships between species mean values of drought frequency
167 during each season and life habitat (annual or perennial) were tested using Firth's

168 penalized-likelihood logistic regressions. Because demographic histories caused by ancestry
169 can confound trait - environment associations, we then tested for the relationships between
170 drought frequency and life history while controlling for relationships between species using

171 phylogenetic logistic regressions.

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 *Heliphila* GBIF records, 6634 were for species with reported life history
178 (Mummenhoff et al., 2005), 3653 had geospatial data, 3627 did not have geospatial issues,
179 3460 were located on pixels classified as land having drought measurements, 3457 were
180 located in Africa, 3162 were not duplicated. After all filtering steps, 2192 records for 42
181 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. *Heliphila rigidiuscula* had the
183 most records, 201, and *Heliphila cornellsbergia* the fewest, 2 (Table S1).

184 There were clear visual differences between the distributions of the 960 annual and the
185 1232 perennial *Heliphila* 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 the
187 Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the
188 occurrences of perennials extended to the east coast of South Africa (Figure 2b).

189 The frequency of drought varied considerably across the ranges of *Heliphila* 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

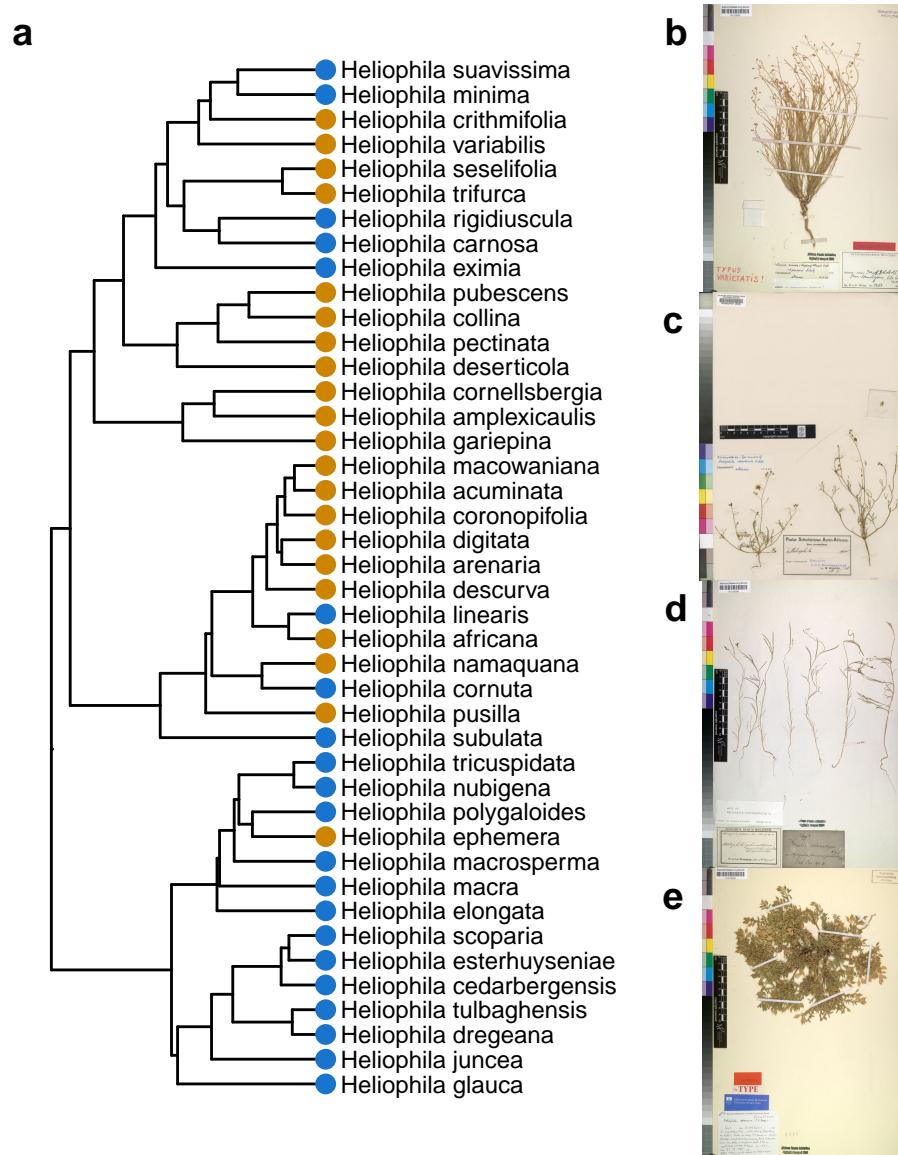


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. Example herbaria specimens accessed via GBIF of (a) *H. minima*, (b) *H. deserticola*,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

195 regions. In the Cape phytogeographic region there was finer scale heterogeneity in drought
196 frequency during the summer.

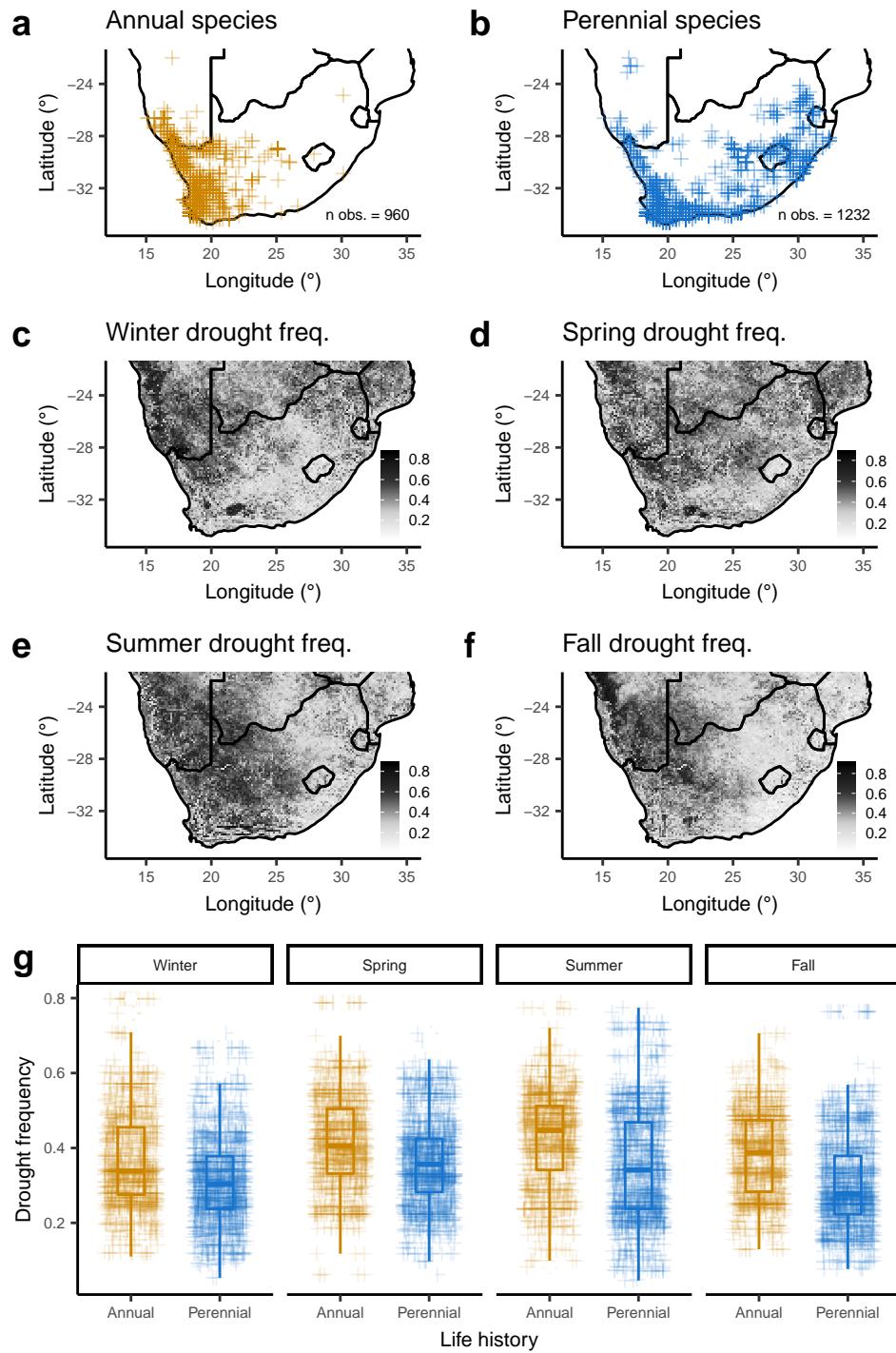


Figure 2. Locations of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall. (g) Drought frequencies during each season observed at the collection sites of *Heliophila* records.

Theory has predicted that annuality should be adaptive in places where stresses such as drought are more common. Conversely, perenniability should be adaptive in places where such stresses are less frequent. We found that the frequency of drought was significantly higher at the locations of occurrence records for annual species. In terms of raw observation records (Figure @??fig:mapsboxplotsg), the frequency of drought was significantly higher at the location of annuals during the winter ($t = 10.65, p = 0.00$), spring ($t = 10.73, p = 0.00$), summer ($t = 12.67, p = 0.00$), and fall ($t = 15.26, p = 0.00$). Because raw occurrence records do not account for variation in the number of records per species (Table S1), we also tested whether mean drought frequency values of each species were significantly different between annuals and perennials by a Firths-penalized logistic regression. We found that the mean drought frequencies were significantly higher ($\alpha = 0.05$) in annual species during the spring, summer, and fall (Table 1, Figure 3a). We further tested whether annual species are found in places where droughts occur more frequently while controlling for the phylogenetic relatedness of *Heliophila* species. This is important, because environmental differences in species distributions can be confounded with demographic history caused by ancestry. We found that while controlling for phylogeny, the mean drought frequencies were significantly higher ($\alpha = 0.05$) in annual species during the spring, summer, and fall (Table 1, Figure 3a). These findings indicate that common ancestry alone does not explain differences in the drought frequencies experienced in the environments of annual and perennial *Heliophila*.

The preceding results indicated that annual species are found in environments where droughts are significantly more frequent, especially in the summer and fall. Classic life history theory hypothesizes that annuality reflects adaptation to such environments because it allows species to escape stressful conditions. If this is the case, we would expect that annuals spend the drought-prone seasons of summer and fall as seeds. To test this hypothesis, we compared the dates of occurrence records between annual and perennial *Heliophila* species. The distributions reveal a considerable difference in the timing of observation of these two life histories. In comparison to perennials, which appear to be collected throughout the year,

Table 1

Logistic regressions between life history, and the mean drought frequency observed at herbaria collection sites of Heliophila species the winter, spring, summer, and fall.

Predictor	Estimate [‘]	P [‘]	Estimate*	P*
Intercept	2.2575	0.1739	0.7231	0.6636
Winter drought freq.	-6.7484	0.1661	-1.5452	0.7274
Intercept	4.5594	0.0443	5.0107	0.0534
Spring drought freq.	-11.7895	0.0423	-12.9014	0.0464
Intercept	7.1742	0.0011	7.7093	0.0054
Summer drought freq.	-18.2999	0.0010	-19.9056	0.0042
Intercept	6.4226	0.0029	7.0162	0.0082
Fall drought freq.	-19.0512	0.0026	-20.8174	0.0067

Note. ‘ = Firth’s penalized logistic regression. * = Phylogenetically constrained logistic regression. Annual species were scored as 0 and perennial species as 1.

224 annuals are almost exclusively observed during the spring (Figure 3b). The differences
 225 between the distribution of collection dates were significant by all tests (ks.test D = 0.25, p =
 226 0; bartlett.test K2 = 503.18, p = 0.00) This is consistent with a model of life history in which
 227 annual species flower in the spring, set seed, senesce, and die before the summer. Thus, these
 228 annual species are likely to remain dormant during the summer and fall, when drought is the
 229 strongest predictor of the distributions of annual and perennial life histories (Figure 3a).

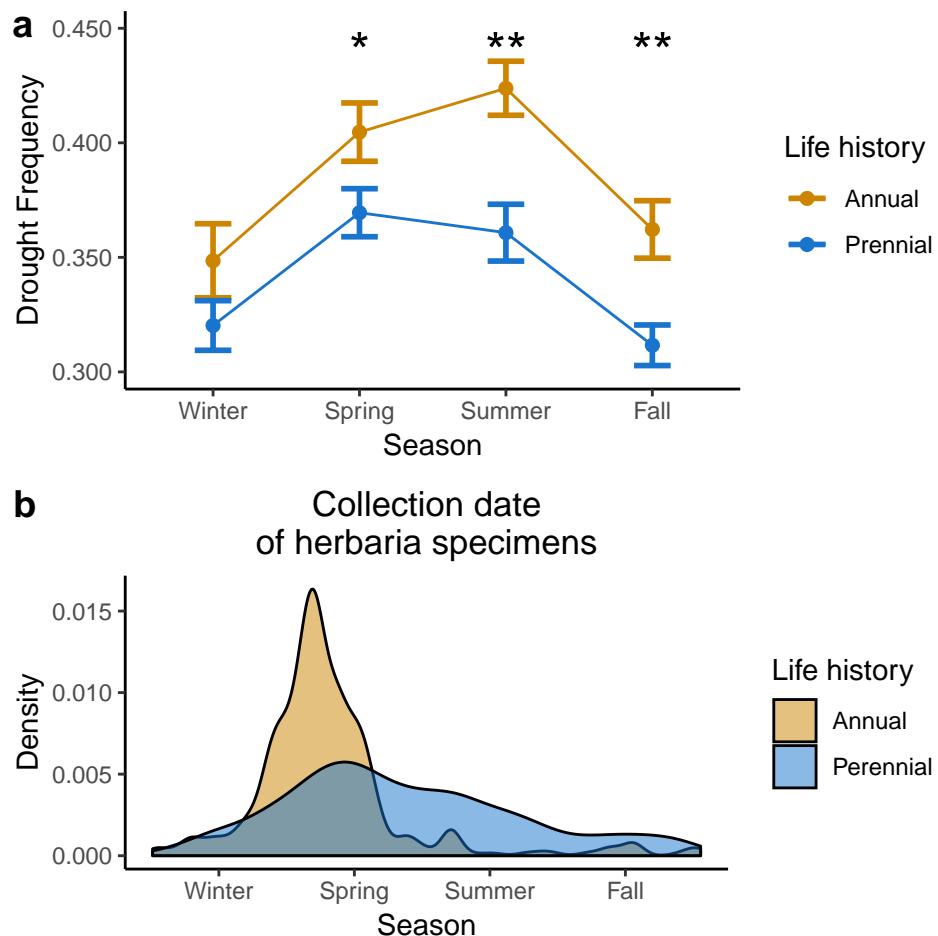


Figure 3. Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (B) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

230

Discussion

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

We cannot eliminate the possibility that confounding traits or environmental variables are the causative factors explaining variation in the distributions of annual and perennial species. Nevertheless, these results reveal quantitative support for the classic prediction that annual species are found in environments that experience more frequent drought than perennial species. These findings complement previous reports of qualitative associations between annuality with environments characterized as having increased aridity (Evans et al., 2005), alternative precipitation defined habitats (Datson et al., 2008; Morishima et al., 1984), or greater unpredictability (Cruz-Mazo et al., 2009). However, to our knowledge this is the first study to demonstrate a significant association between life history and drought in a phylogenetic context informed by large scale species distribution data and long term drought measures.

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

263 which represents a significant advance over relying on personal observations to characterize
264 species distributions.

265 These findings support classical theoretical predictions about the adaptive value of
266 annual and perennial life history strategies. Taken together, they suggest that in *Heliophila*,
267 annual species are adapted to environments with increased summer droughts by avoiding
268 these seasons in a dormant seed phase of their life cycle. They also suggest that perenniability
269 is adaptive in environments where droughts are less frequent. While most previous work has
270 focused on describing the evolutionary origins of annuality (Andreasen & Baldwin, 2001;
271 Barrett et al., 1996; Conti, Soltis, Hardig, & Schneider, 1999; Friedman & Rubin, 2015;
272 Verboom, Linder, & Stock, 2004) there are at least a few other cases where perenniability
273 appears to have arisen from an annual ancestor (Bena, Lejeune, Prosperi, & Olivieri, 1998;
274 Tank & Olmstead, 2008). And while early theory predicted selection for annuality when
275 adult mortality is high (Stearns, 1992), we also find evidence that the transition to
276 perenniability could be explained by historical drought regimes. The phylogeny reveals several
277 transitions from annual to perennial life history (Figure 1a) and that perennials distributions
278 extend into regions where drought frequency is low (Figure 2b, Figure S1). Perennials may be
279 able to outcompete annual relatives in environments where the infrequency of drought
280 favors strategies that allow plants to benefit from growth over many seasons. It may also
281 indicate that annuals rely on drought as a source of disturbance for seedling recruitment
282 when competing with perennials (Corbin & D'Antonio, 2004). Indeed, no annual species
283 were observed in the low drought regions of east South Africa 2a, Figure S1).

284 These findings suggest that species with locally adapted life history strategies could be
285 threatened by rapidly changing drought regimes (Dai, 2011). This could have impacts on
286 ecosystem functioning if the composition of annual and perennial species changes as a
287 response (Garnier, Cordonnier, Guillerm, & Sonié, 1997; Roumet, Urcelay, & Di'az, 2006).
288 Furthermore, the frequency of drought may be an important factor when considering the use

289 of perennial cropping sysyems (Lelièvre & Volaire, 2009; Parry, Flexas, & Medrano, 2005).

290 In conclusion, we find strong support for classic life history theory which predicts that
291 annuality is adaptive environments where droughts occur more frequently. Additionally, we
292 report evidence consistent with a life history model in annuals in which they escape drought
293 prone seasons during the seed phase of their life cycle. Finally, we find evidence that the
294 distributions of perennial lineages may indicate a competitive advantage in areas where
295 droughts are infrequent. More broadly, this work demonstrates the power of emerging data
296 to address outstanding classic hypotheses in ecology and evolution.

297

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492

Supplement

493 **Images used.** <https://www.gbif.org/occurrence/1099023487>
494 <https://www.gbif.org/occurrence/1057389408> <https://www.gbif.org/occurrence/1099023562>
495 <https://www.gbif.org/occurrence/1099023490>

496 **Software used.** We used R (Version 3.5.1; R Core Team, 2018) and the R-packages
497 *ape* (Version 5.2; Paradis & Schliep, 2018; Orme et al., 2018; Soetaert, 2018), *bindrcpp*
498 (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme et al., 2018), *coda* (Version 0.19.2;
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500 (Version 0.7.8; Wickham et al., 2018), *forcats* (Version 0.3.0; Wickham, 2018a), *gee* (Version
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506 & Ripley, 2002), *Matrix* (Version 1.2.15; Bates & Maechler, 2018), *MCMCglmm* (Version
507 2.26; Hadfield, 2010), *mvtnorm* (Version 1.0.8; Genz & Bretz, 2009), *papaja* (Version
508 0.1.0.9842; Aust & Barth, 2018), *phylolm* (Version 2.6; Ho & Ane, 2014), *phytools* (Version
509 0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry & Wickham, 2018), *raster* (Version 2.8.4;
510 Hijmans, 2018), *readr* (Version 1.2.1; Wickham et al., 2017), *shape* (Version 1.4.4; Soetaert,
511 2018), *sp* (Version 1.3.1; Pebesma & Bivand, 2005), *stringr* (Version 1.3.1; Wickham, 2018b),
512 *tibble* (Version 1.4.2; Müller & Wickham, 2018), *tidyverse* (Version 0.8.2; Wickham & Henry,
513 2018), and *tidyverse* (Version 1.2.1; Wickham, 2017) for all our analyses.

514

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.

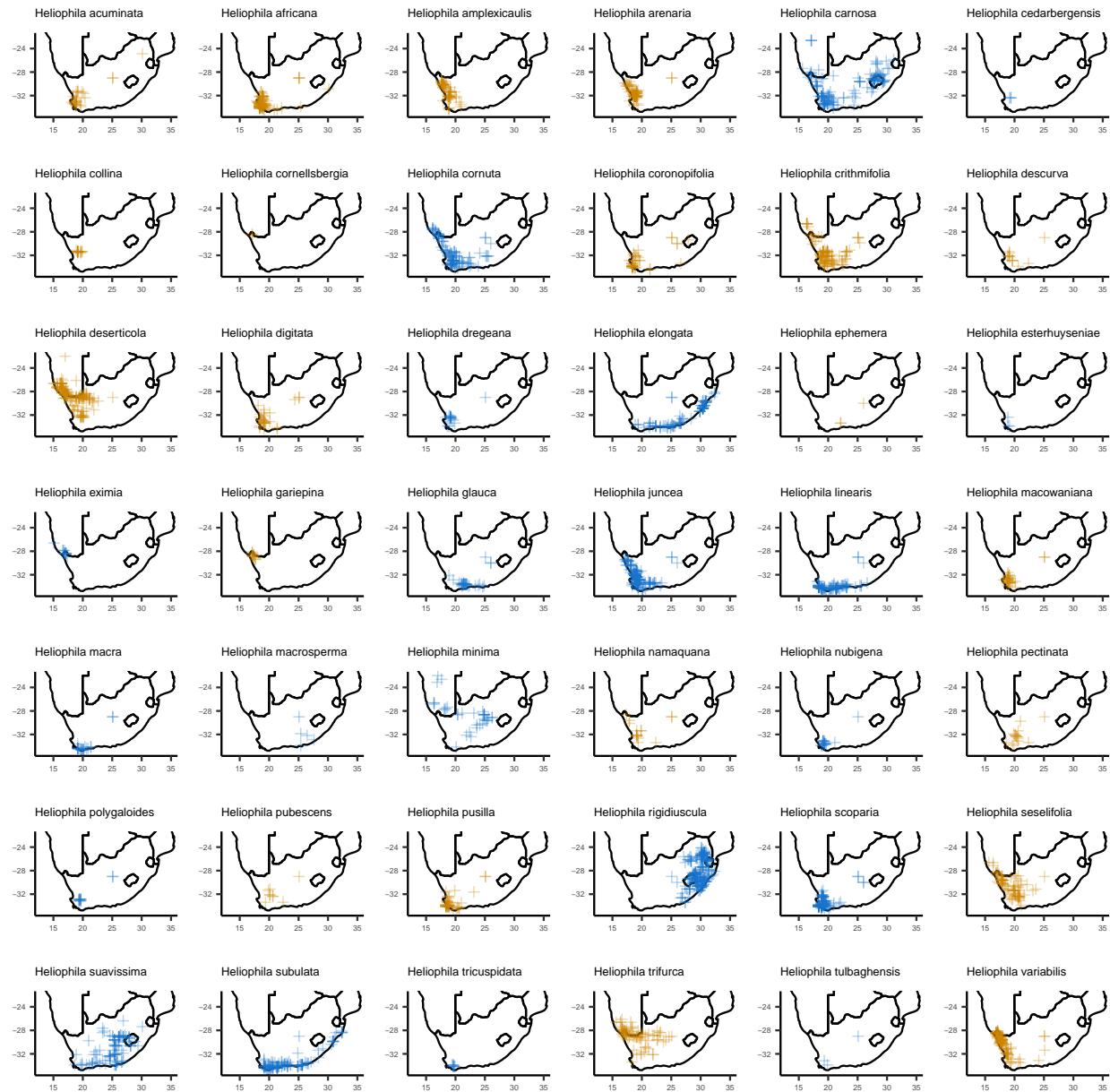


Figure S1. Maps of occurrence records for individual species. Orange points indicate annual species. Blue points indicate perennial species.