

¹ Drought regimens predict 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 biology
14 and ecology. Early theory predicted that for plants, annual and perennial life histories reflect
15 adaptation to environments that experience alternative drought regimens. Nevertheless,
16 empirical support for this hypothesis from comparative analyses remains lacking.

17 Here, we test classic life history theory in *Heliophila* (Brassicaceae), a diverse genus of
18 flowering plants native to Africa, controlling for phylogeny and integrating 34 years of
19 satellite-based drought detection with 2,192 herbaria occurrence records.

20 We find that the common ancestor of *Heliophila* species was likely an annual, and that
21 perenniability and annuality have repeatedly evolved, an estimated seven and five times,
22 respectively. By comparing historical drought regimens, we show that annuals occur in
23 environments where droughts are significantly more frequent than perennial species. We also
24 provide evidence that annual plants adapt to predictable drought regimens by escaping
25 drought prone seasons as seeds.

26 These results yield compelling support for longstanding theoretical predictions by
27 revealing the importance of drought frequency and predictability to explain plant life history.
28 More broadly, this work highlights scalable approaches integrating herbaria records and
29 remote sensing to address outstanding questions in evolutionary ecology.

30 *Keywords:* drought adaptation, herbaria records, *Heliophila*, life history evolution,
31 phylogeography, remote sensing

32 Drought regimens predict life history strategies in *Heliophila*

33 **Introduction**

34 Understanding the causes of life history variation and climate adaptation are
35 longstanding goals of ecology and evolutionary biology (Raunkiaer, 1905; Turesson, 1925;
36 Clausen *et al.*, 1948; Cole, 1954). In plants, life histories are especially diverse, with some
37 species completing their life cycle in a number of weeks to others that live for thousands of
38 years (Brown, 1996). Along this continuum in angiosperms an important division exists
39 distinguishing annuals which complete their seed to seed life cycle within a single year from
40 perennials which can persist over multiple years. Annual plants do not need to survive
41 through the full range of seasonal environmental variation and spend at least some portion of
42 the year as a seed where they are relatively protected from environmental stress. In contrast,
43 perennial plants can continue vegetative growth over multiple years and must survive
44 conditions experienced during all seasons but can also benefit from competitive advantages
45 and, if iteroparous, multiple bouts of reproduction. These represent fundamentally different
46 life history strategies and predicting their occurrence is important for community, ecosystem,
47 and agricultural ecology. However, the environmental factors that explain their evolution
48 and distributions remain empirically unresolved (Friedman & Rubin, 2015).

49 Classical theory predicts shorter life spans in environments where adult mortality is
50 high (Charnov & Schaffer, 1973; Stearns, 1992; Franco & Silvertown, 1996). Because lack of
51 water is one of the greatest threats to survival during vegetative or reproductive growth in
52 plants, this theory has been extended to the hypothesis that annuality is adaptive when it
53 allows plants to escape drought (Cody *et al.*, 1975; Schaffer & Gadgil, 1975). Indeed,
54 adaptation to drought, defined as episodes of increased aridity causing plant stress
55 (Passioura, 1996), is often invoked as an explanation for the success of annual species, though
56 drought adapted perennials are also well known (Raunkiaer, 1905). And while a few cases

57 are cited where annuality appears to be more common in environments with greater aridity
58 (Stebbins Jr, 1952; Morishima *et al.*, 1984), this hypothesis has yet to be supported while
59 controlling for the effect of common ancestry (phylogeny) on life habit. In one previous study
60 where this question was addressed phylogenetically, (Evans *et al.*, 2005) annuals were not
61 found to be associated with environments that experience more drought. This could be
62 explained by the relatively small number of species studied and the reliance on a limited
63 number of weather stations to characterize environments, highlighting the need to develop
64 more scalable methods to study the geographic distributions of traits such as life history.
65 Thus, in this study we leverage thousands of herbaria specimens among dozens of species
66 and high-resolution remote sensing to study the distributions and environmental factors
67 potentially driving the evolution and distribution of life history.

68 It is also critical to consider another dimension of drought adaptation: the expectation
69 that annuality is most adaptive when droughts are not only frequent but also predictable.
70 That is, when the frequency of drought is particularly high during certain seasons. Such
71 predictability is important for selection to favor an escape strategy during those seasons
72 which are particularly drought prone. While there has been at least one example of annuality
73 associated with environments qualitatively classified as “predictable” in a general sense
74 (Datson *et al.*, 2008), the seasonal predictability of drought experienced by annuals has yet
75 to be rigorously studied. As such, further empirical work is needed to support the model of
76 annuality as a mechanism of drought adaptation via escape from drought prone seasons.
77 Here we examine herbarium collection dates to ask whether annuals indeed exhibit evidence
78 of an escape strategy from seasons with elevated drought frequency.

79 In addition to drought escape in annuals as a mechanism of adaptation to frequent and
80 predictable droughts, droughts may be necessary for the success of annuals more generally by
81 acting as episodes of disturbance that provide opportunities for annuals to establish and
82 compete with sympatric perennial species. Indeed, there is evidence that perennials dominate

83 in environments where disturbance events are infrequent (Rees & Long, 1992; Corbin &
84 D'Antonio, 2004; Clary, 2012). The resulting prediction from this hypothesis is that in the
85 absence of frequent drought, perenniability should evolve. However, little is known about this
86 component of life history evolution because previous work has almost entirely focused on the
87 origins of annuality rather than perenniability (Friedman & Rubin, 2015). This highlights the
88 need to study taxa which have seen transitions from annual to perennial life histories as well.

89 Here we combine a long-term global dataset of satellite detected drought events with
90 metadata from natural history collections to test these classic hypotheses within the African
91 endemic mustard genus, *Heliophila* L. (Brassicaceae). If annuality is an adaptive strategy
92 allowing plants to escape drought prone seasons, then drought frequency should predict the
93 distribution of life history strategies across landscapes, and annual species should be more
94 commonly associated with drought prone regions than perennial species. Additionally, if
95 perenniability offers competitive advantage in the absence of drought, associations between life
96 history and drought frequency should be significant when phylogenies include transitions
97 from annual to perennial life history strategy. Finally, if annual species have adapted to
98 escape predictably drought prone seasons, observations of growing annual species
99 (i.e. occurring in forms other than seed) should be rare during seasons when drought
100 frequency is highest. Phylogenetic relatedness can influence tests of associations between
101 species' traits and their environments by confounding common environments caused by
102 selection from common environments caused by ancestry. (Felsenstein, 1985; Barrett *et al.*,
103 1996). Therefore, we assessed the relationship between life history distribution and drought
104 frequency while controlling for phylogeny.

105

Materials and Methods

106 **Data**

107 **Data availability.** All analyses were performed using R. All data and the source

108 code to produce this manuscript are available at <https://github.com/greymonroe/heliophila>.

109 **Life history data for *Heliophila*.** *Heliophila* is a genus of flowering plants

110 endemic to southern Africa including the Cape Floristic and Succulent Karoo Regions. These

111 are among the most botanically diverse environments on Earth and the *Heliophila* species

112 occurring there are considered to be among the most phenotypically diverse genera of the

113 family Brassicaceae (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). This genus includes

114 both perennial and annual species, and transitions between life history strategy may have

115 occurred multiple independent times (Appel & Al-Shehbaz, 1997; Mummenhoff *et al.*, 2005).

116 Furthermore, the fine scale climatic heterogeneity of southern Africa is ideal for studying the

117 distribution of traits in relation to environmental parameters (Sayre *et al.*, 2013). We used

118 life histories reported by Mummenhoff *et al.* (2005), grouping species into annual or

119 perennial life history categories. Perenniality was defined as any form of perennial life

120 history (e.g., herbs, shrubs, mixed, etc). Because the nature of species reported with mixed

121 traits were unknown (i.e. plasticity vs. genetic variation), we classified these species here as

122 perennial since they can maintain vegetative across multiple years at least to some capacity.

123 ***Heliophila* occurrence records.** To characterize the distributions of annual

124 (studied here, n = 21) and perennial (studied here, n = 21) *Heliophila* species, all (8670)

125 records for the genus *Heliophila* were downloaded from the Global Biodiversity Information

126 Facility (gbif.org) on July 21, 2018 (GBIF, 2018). Herbaria records such as these provide a

127 rich data sources to characterize the geographical distributions of species (Thiers, 2016;

128 Willis *et al.*, 2017; Lang *et al.*, 2019). And as they become digitized (Soltis, 2017), herbaria

129 collections have been used to study relationships between trait distributions, geography, and

130 climate (Davis *et al.*, 2015; Stropp *et al.*, 2016; Wolf *et al.*, 2016; Václavík *et al.*, 2017).

131 **Sequence data for phylogeny.** An alignment of ITS I and II sequences for 21

132 annual and 21 perennial *Heliophila* species was obtained from the authors of Mandáková *et*

¹³³ *al.* (2012). Individual ITS I and II sequences for *Aethionema grandiflorum*, *Alliaria petiolata*,
¹³⁴ *Cardamine matthioli*, *Chamira circaeoides*, and *Rorippa amphibia* were downloaded from
¹³⁵ Genbank.

¹³⁶ **Satellite-detected drought data.** Remotely sensed data is a powerful tool for
¹³⁷ characterizing seasonal patterns in drought because it is less limited in spatial and temporal
¹³⁸ scope and resolution than weather stations or field observations (AghaKouchak *et al.*, 2015).
¹³⁹ From an ecological perspective, droughts are best defined as episodes of plant stress caused
¹⁴⁰ by elevated aridity (Passioura, 1996). Thus remote sensing offers the additional benefit for
¹⁴¹ studying drought as an agent of natural selection because plant stress caused by drought can
¹⁴² be observed from space (Kogan, 1995a). The remotely sensed Vegetative Health Index (VHI)
¹⁴³ is one such metric, which detects landscape scale reductions in plant cover and temperature
¹⁴⁴ conditions characteristic of drought (Kogan, 2001). Generated from data collected by NOAA
¹⁴⁵ AVHRR satellites since 1981, the VHI is a composite index combining Normalized Difference
¹⁴⁶ Vegetation Index (NDVI) derived quantification of vegetative stress (Vegetative Condition
¹⁴⁷ Index - VCI) with temperature stress indicated by anomalies in thermal spectra
¹⁴⁸ (Temperature Condition Index - TCI). These indices were developed to create an unbiased
¹⁴⁹ quantification of drought across ecosystem types. The VHI of year y during week w of [1, 52]
¹⁵⁰ at pixel i is derived from the following equations, where n is the number of years observed.

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

¹⁵¹ Low values of VCI indicate episodes when plant cover is particularly low for a given
¹⁵² location during a given time of the year. Thus, it controls for the location and season in
¹⁵³ quantifying plant stress.

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

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

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

156 By combining VCI and TCI, the VHI distinguishes drought from other forms of vegetative
157 stress (Kogan, 1995b). The use of the VHI to detect drought has been validated globally and
158 across ecosystem types (AghaKouchak *et al.*, 2015), including in southern Africa, the focal
159 region of this study (e.g. Figure S1). To date, the VHI has most often been applied for
160 evaluating drought risk for agricultural research (e.g., Rojas *et al.*, 2011; Kogan *et al.*, 2016).
161 But it also presents a tool to study seasonal patterns in the frequency of drought across
162 environments and to test hypotheses about the effect of drought on ecological and
163 evolutionary processes (Kerr & Ostrovsky, 2003). As such, the VHI has been applied recently
164 to study drought related ecology of natural species and proven useful for predicting
165 intraspecific variation in drought tolerance traits and genes (Mojica *et al.*, 2016; Dittberner
166 *et al.*, 2018; Monroe *et al.*, 2018b). Here, we accessed VHI data at $16km^2$ resolution from
167 1981 to 2015 (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) to
168 characterize the seasonal drought frequencies experienced by annual and perennial *Heliphila*
169 species across their native range of southern Africa.

170 **Analyses**

171 **Drought frequency calculations.** To characterize drought regimens across the
172 distributions of annual and perennial species of *Heliphila*, we calculated drought during
173 different seasons at the location of observations for *Heliphila* records using the VHI.
174 Specifically, we created maps of the frequencies of observing drought conditions between
175 years (VHI<40, NOAA) during the winter (quarter surrounding winter solstice), spring
176 (quarter surrounding spring equinox), summer (quarter surrounding summer solstice) and

177 autumn (quarter surrounding autumn equinox) from 1981 to 2015 across the range of
178 *Heliophila*. From these maps, the drought frequency (the number of times drought is
179 observed divided by the total number of years, 34) during the winter, spring, summer, and
180 autumn were extracted for the locations of all GBIF records.

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

- 183 • records for species with reported life history
- 184 • records with geospatial data
- 185 • records without known geospatial coordinate issues (i.e., coordinates reported are those
186 of herbarium)
- 187 • records from collection sites classified as land pixels in the VHI dataset
- 188 • records from Africa (to exclude locations of cultivation)
- 189 • records without duplicates (i.e., identical species, location, collection date)

190 Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history
191 (Mummenhoff *et al.*, 2005), 2856 had geospatial data, 2833 did not have geospatial issues,
192 2684 were located on pixels classified as land having drought measurements, 2543 were
193 located in Africa, 2192 were not duplicated.

194 **Phylogeny construction and ancestral state estimation.** Outgroup (194)
195 *Aethionema grandiflorum*, *Alliaria petiolata*, *Cardamine matthioli*, *Chamira circaeoides*, and
196 *Rorippa amphibia*) and ingroup *Heliophila* ITS I and II sequences were aligned using
197 MAFFT (Katoh *et al.*, 2002) with strategy G-INS-I, offset value 0.1, and all other options
198 set as default. The *GTR + Γ* model of nucleotide substitution was determined to best fit the
199 data based on AIC using jModelTest2 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012). A
200 maximum clade credibility tree with branch lengths as relative time was estimated by
201 summarizing data from six runs of 100,000,000 generations of Bayesian Markov chain Monte

202 Carlo conducted in BEAST 2 (Bouckaert *et al.*, 2014). Model selection and phylogenetic
203 analyses were conducted through the CIPRES Science Gateway (Miller *et al.*, 2010).
204 Ancestral state estimation was performed in R using the package phytools (Revell, 2012) to
205 generate 10,000 stochastic character maps simulated under an equal rates model of character
206 evolution for the trait life habit (annual or perennial).

207 Comparison of drought frequency between annual and perennial species.

208 To evaluate the hypothesis that annual and perennial life history strategies reflect
209 adaptations to alternative drought regimens, we tested the corresponding prediction that the
210 observed distributions of annual and perennial *Helophilus* species would be significantly
211 associated with historic drought frequency. We tested for a relationship between drought
212 frequency and life history, season, and their interaction by analysis of variance while
213 including species as a random effect using the lme4 package in R (Bates *et al.*, 2014) and
214 compared annuals and perennials using Tukey adjusted post-hoc contrasts. We next
215 calculated the mean drought frequency during the winter, spring, summer and autumn for
216 each species. Because shared evolutionary history of closely related species can lead to
217 spurious associations between traits and environments (Felsenstein, 1985), we tested for a
218 relationship between life history strategy and drought frequency while controlling for
219 phylogeny using phylogenetic logistic regression (Ives & Garland, 2010). This statistical
220 approach is designed to control for the confounding effects of common ancestry's influence on
221 demographic features such as geospatial relationships when addressing hypotheses about the
222 role of natural selection on trait distributions.

223 Collection dates. To test the hypothesis that annual species have adapted to

224 escape drought prone seasons as seeds, collection dates for herbarium specimens were
225 compared between annual and perennial species. Comparisons of distributions were made by
226 Two-sample Kolmogorov-Smirnov test and Barlett variance test.

Results

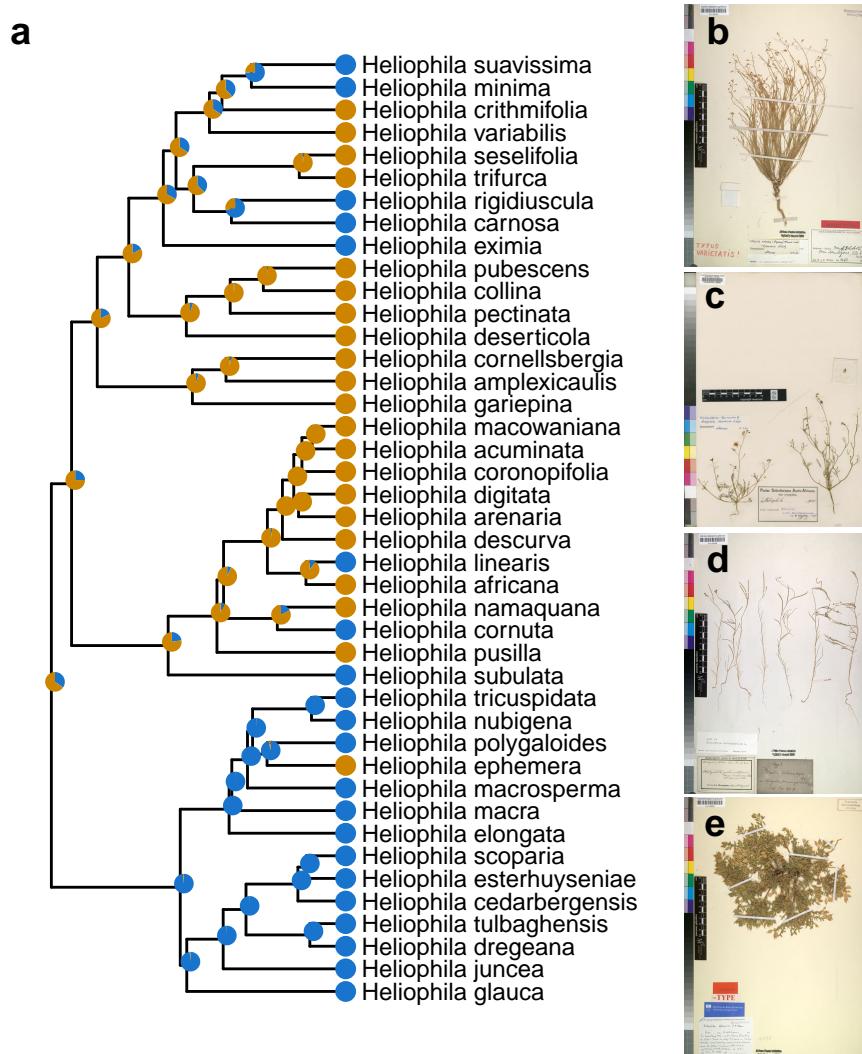


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. At internal nodes, pie charts indicate the estimated posterior probability of being annual versus perennial. Example herbaria specimens accessed via GBIF of (b) *H. minima*, (c) *H. deserticola*, (d) *H. coronopifolia* and (e) *H. ephemera*. Images (b,d,e) courtesy of The Bavarian Natural History Collections (CC BY-SA 4.0) and (c) The London Natural History Museum (CC BY 4.0). Links to images are found in the supplement.

228 The topology of the estimated *Heliophila* phylogeny was consistent with previous
229 studies (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). Based on 10,000 stochastic
230 character maps simulated under an equal rates model of character evolution in life history,
231 an average of approximately seven changes from annual to perennial and five changes from
232 perennial to annual are observed per stochastic character map (Figure 1a). These results
233 suggest that the ancestral state of *Heliophila* was annual and that both character states have
234 arisen independently multiple times.

235 After all filtering steps, 2192 records for 42 species (Figure 1, Table S1) passed for
236 further analyses. The number of samples varied between species, with a mean of 52.19
237 samples per species. *H. rigidiuscula* had the most records, 201, and *H. cornellsbergia* the
238 fewest, 2 (Table S1).

239 There were clear visual differences between the distributions of the 960 annual and the
240 1232 perennial *Heliophila* observation records (Figure 2, Figure S2). While annual species
241 were generally found in the western regions of South Africa and Namibia, primarily in the
242 Cape Floristic Region and Succulent Karoo (Figure 2a), the occurrence of perennials
243 extended to the southern and eastern coast of South Africa (Figure 2b).

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

252 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), a mixed-model analysis of variance which included species as random effect revealed a significant relationship between drought frequency and life history ($p < 0.01$), season ($p < 0.01$) and their interaction ($p < 0.01$) (Table S2). Post-hoc contrasts showed that the frequency of drought was significantly higher at the location of annuals during the summer (z ratio = 3.93, $p = < 0.01$), and autumn (z ratio = 4.06, $p < 0.01$). Because a comparison across all occurrence records does not account for variation in the number of records per species (Table S1) or species relatedness (Figure 1a), we also tested whether mean drought frequency values of each species were significantly different between annuals and perennials using phylogenetic logistic regression. We found that the mean drought frequencies were significantly higher ($\alpha = 0.05$) in annual species during the spring, summer, and autumn (Table 1, Figure 3a,b). These findings indicate that common ancestry alone does not explain differences in the drought frequencies experienced between the environments of annual and perennial *Heliophila*.

The preceding results indicate that annual species are found in environments where droughts are significantly more frequent, especially in the summer and autumn. Classic life 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 autumn as seeds. To test this hypothesis, we compared the dates of occurrence records between annual and perennial *Heliophila* species. The distributions reveal a considerable difference in the timing of observation of these two life histories. In comparison to perennials, which appear to be collected throughout the year, annuals are almost exclusively observed during the winter and spring (Figure 3b). The differences between the distribution of collection dates were significant by all tests ($ks.test D = 0.25, p < 0.01$; $bartlett.test K2 = 503.18, p < 0.01$) 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

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 autumn*

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
Autumn drought freq.	-20.8174	0.0067

Note. Annual species were scored as 0 and perennial species as 1.

²⁸⁰ dormant during the summer and autumn, when drought is the strongest predictor of the
²⁸¹ distributions of annual and perennial life histories (Figure 3a).

²⁸²

Discussion

²⁸³ To test the hypothesis that annual and perennial plants reflect adaptation to
²⁸⁴ alternative drought environments we examined the distributions of life history strategies in
²⁸⁵ 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 *Heliphila* 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, building on 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

312 history distribution. Indeed, we were able to use 2192 occurrence records to study 42 species,
313 which represents a significant advance over relying on personal observations to characterize
314 species distributions.

315 These findings empirically support classical theoretical predictions about the adaptive
316 value of annual and perennial life history strategies. Taken together, they suggest that in
317 *Heliophila*, annual species are adapted to environments with predictable droughts by
318 escaping drought prone seasons during the dormant seed phase of their life cycle. They also
319 suggest that perenniability is adaptive in environments where droughts are less frequent.

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

335 These findings suggest that species with locally adaptive life history strategies could be
336 threatened by rapidly changing drought regimens (Dai, 2011). In light of the findings here,
337 forecasted reductions in rainfall across eastern South Africa (SAWS & WRC, 2017) could be

338 particularly impactful to plant community compositions. Here we found that this region is
339 currently dominated by derived perennial species of *Heliophila*. However, a scenario in which
340 droughts become more frequent in this region may allow for the establishment of annuals.
341 Such changes in selection patterns and shifts in plant functional diversity could have impacts
342 on ecosystem functioning and processes such as carbon cycling (Garnier *et al.*, 1997; Roumet
343 *et al.*, 2006; Monroe *et al.*, 2018a). Furthermore, the changes in frequency of drought may be
344 an important factor when considering the use of perennial cropping systems (Parry *et al.*,
345 2005; Lelièvre & Volaire, 2009).

346 In conclusion, we find strong support for classic life history theory that predicts that
347 annuality is adaptive in environments with frequent and predictable droughts. We report
348 evidence consistent with a life history model in annuals in which they escape drought prone
349 seasons during the seed phase of their life cycle. We also find evidence that the distributions
350 of perennial lineages may indicate a competitive advantage in areas where droughts are
351 infrequent. More broadly, this work highlights the irreplaceable value of natural history
352 collections and demonstrates the power of combining such information with large scale
353 remote sensing data to address outstanding classic hypotheses in ecology and evolution.

354

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358

Author contributions

359 JGM, BG, KGT and JKM contributed to the design of the research, interpretation,
360 and writing the manuscript. JGM, BG, and KGT contributed to the performance of the

361 research and data analysis.

362

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526

Supplement

527 **Notes S1.** Images of herbarium specimens in Figure 1. Used under creative
528 commons licenses, permissions not required. <https://www.gbif.org/occurrence/1099023487>
529 <https://www.gbif.org/occurrence/1057389408>
530 <https://www.gbif.org/occurrence/1099023562>
531 <https://www.gbif.org/occurrence/1099023490>

532

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	Autumn
<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.

Table S2

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	Sum.Sq	Mean.Sq	NumDF	DenDF	F.value	p-value
life history	0.1715	0.1715	1	36.9156	12.2117	0.0013
season	4.3906	1.4635	3	8,718.5058	104.2028	0.0000
life history x season	0.2035	0.0678	3	8,718.5058	4.8301	0.0023

Note. Type III Analysis of Variance Table with Satterthwaite's method

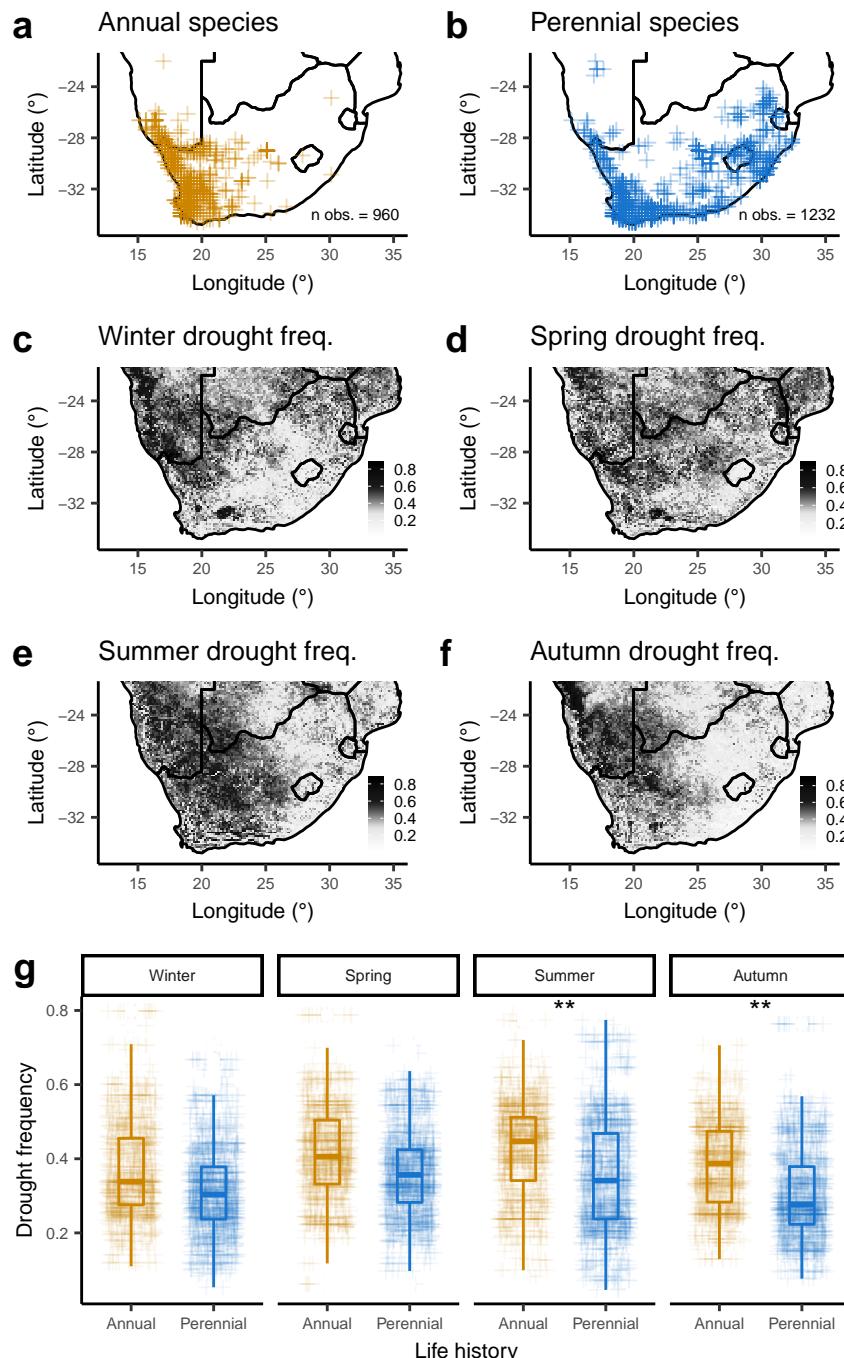


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) autumn detected using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (Post-hoc contrasts annuals and perennials from ANOVA, ** = $p < 0.01$). Boxplots indicate median (horizontal line), first and third quartiles (upper and lower limits of box), and 1.5 times the interquartile range (whiskers). Individual observations are shown by crosshairs. Annual and perennial species are indicated by data colored blue and orange, respectively.

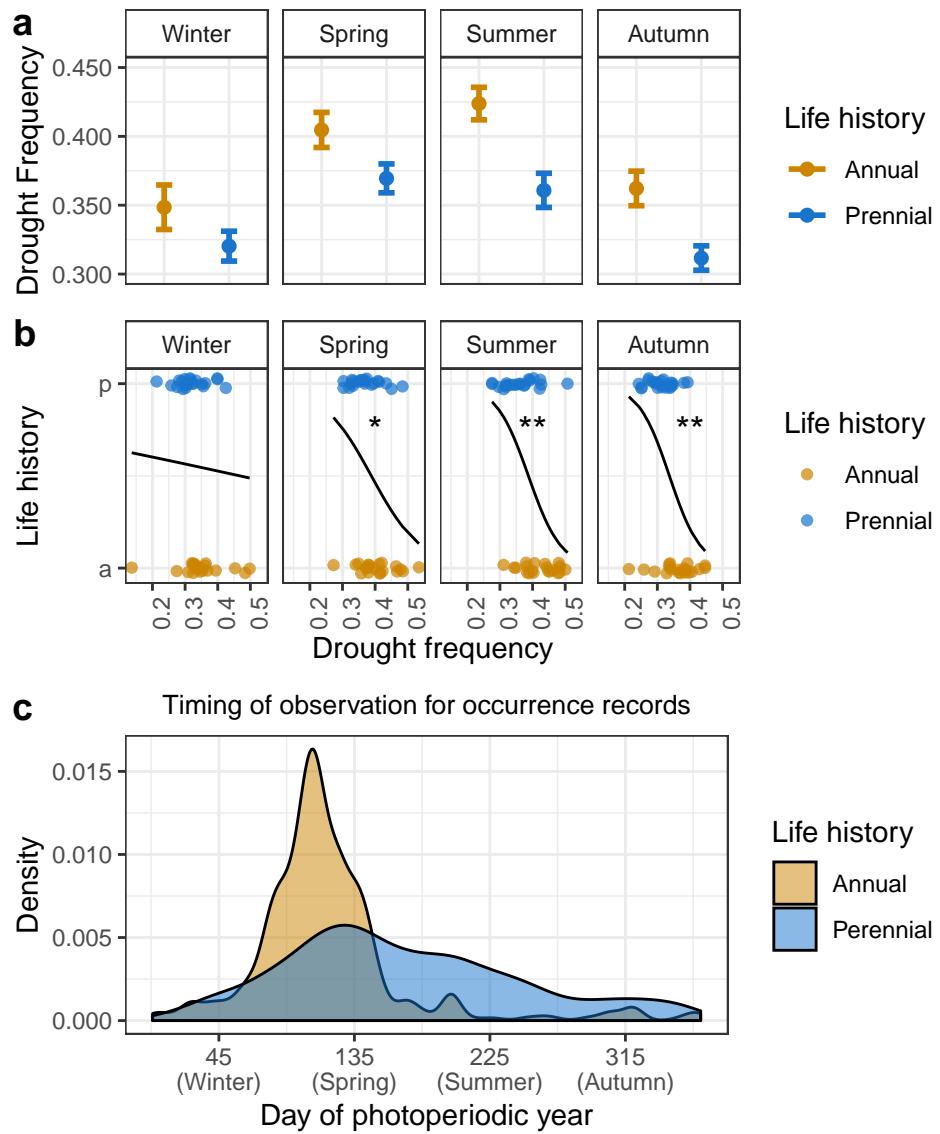


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons calculated at the occurrence locations of GBIF records of annual and perennial species of *Heliophila*. (b) Results from phylogenetic logistic regression, where the line shows the model fit and * = $p < 0.05$, ** = $p < 0.01$. Annuals 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 autumn equinox and winter solstice.

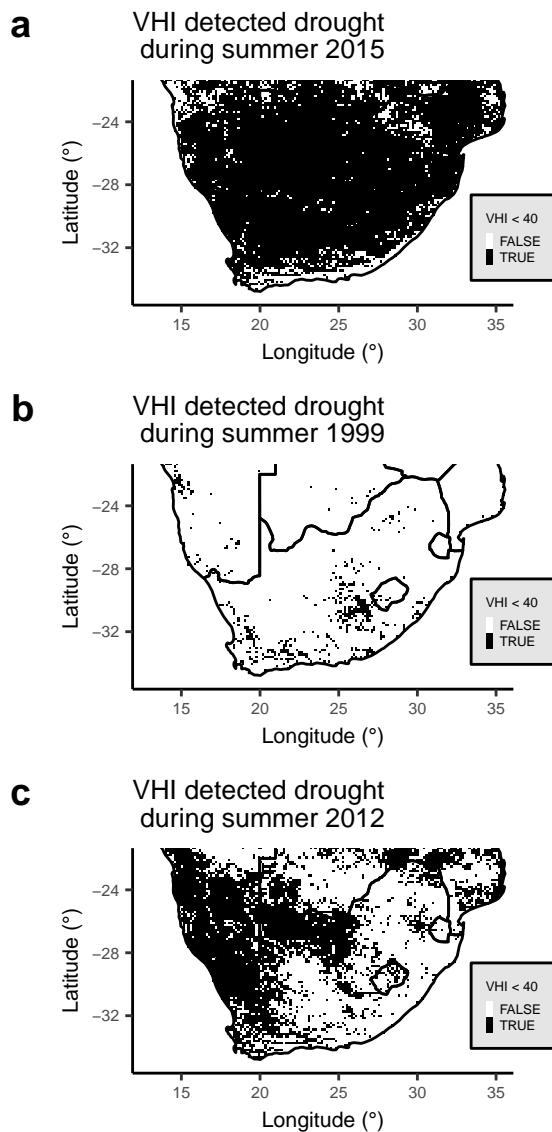


Figure S1. Example years experiencing contrasting degrees of drought in southern Africa. Vegetative Health Index (VHI) values below 40 indicate remotely sensed drought. Drought detection during these years is validated by previously reported precipitation based estimates of drought occurrence (Monyela, 2017) 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. 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.