

¹ Satellite-detected drought frequencies predict plant life history strategies

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11

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 *Heliphila* (Brassicaceae), a diverse genus of flowering plants native to
16 Southern Africa using herbarium occurrence records and satellite-detected drought histories.
17 We find that perennial *Heliphila* species are found in environments where droughts are
18 significantly less frequent compared to annuals. These associations are predictive while
19 controlling for phylogeny, lending support to the hypothesis that drought related natural
20 selection has influenced the distributions of these strategies. Additionally, the difference in
21 drought frequency between annual and perennial species distributions is greatest during the
22 summer and fall, which also appears to be when annuals are in the seed phase of their life
23 cycle based on collection dates of annual species. Together, these findings support traditional
24 hypotheses about the drivers of life history strategy in plants - that perenniability is favored in
25 environments with less frequent drought and annuality in environments with more frequent
26 drought by allowing them to escape drought prone seasons as seeds.

27

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

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30 **Introduction**

31 **Life history variation in plants**

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. In contrast, perennial plants can
40 continue vegetative growth after reproduction and experience all seasons. These represent
41 fundamentally different life history strategies, but the ecological factors that explain their
42 evolution remain unresolved (Friedman & Rubin, 2015).

43 Identifying the drivers of selection for these alternative strategies is important because
44 annuals and perennials have differing impacts on ecosystem functioning. For example,
45 perennials have higher nitrogen concentration and larger specific root length in annuals,
46 which both affect nutrient cycling (Garnier, Cordonnier, Guillerm, & Sonié, 1997; Roumet,
47 Urcelay, & Di'az, 2006). Furthermore, predicting the conditions that favor these strategies in
48 nature is useful for developing more sustainable perennial cropping systems (Lelièvre &
49 Volaire, 2009).

50 Classical theory predict shorter life spans and annuality in environments where adult
51 mortality is high (Charnov & Schaffer, 1973; Franco & Silvertown, 1996; Stearns, 1992). In
52 plants, this has been extended to the hypothesis that annuality is adaptive when it allows

53 plants to escape drought (Schaffer & M, 1975). Lack of water is perhaps the greatest threat
54 to survival during vegetative or reproductive growth and annuals can remain dormant (and
55 protected as a seed) during drought. Thus, environments with greater seasonal drought
56 frequency may select for annual life histories that complete reproduction prior to drought
57 prone seasons. Conversely, environments with less frequent drought may select for perennial
58 species, which may benefit from multiple bouts of reproduction and competitive advantage
59 (Corbin & D'Antonio, 2004). These prediction has been supported by the association of
60 annuality with arid environments in wild rice (Morishima, Sano, & Oka, 1984) and
61 *Oenothera* (Evans, Hearn, Hahn, Spangle, & Venable, 2005). Additionally, annual and
62 perennial species of *Nemesia* were qualitatively associated with winter rather and summer
63 rainfall environments respectively (Datson, Murray, & Steiner, 2008) and annual species of
64 *Scorzoneroidea* were associated with environments classified as unpredictable (Cruz-Mazo,
65 Buidé, Samuel, & Narbona, 2009). These findings provide qualitative evidence supporting
66 the prediction that annual species are found in environments that experience more frequent
67 drought, and vice versa, but whether the history frequency of drought events indeed predicts
68 the distributions annual or perennial life history strategies has yet to be tested.

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

80

Materials and Methods

81 Availability

82 All data and the source code to produce this manuscript are available at

83 <https://github.com/greymonroe/heliophila>.

84 Data

85 **Satellite-detected drought data.** Remotely sensed data is a powerful tool for
 86 characterizing seasonal patterns in drought because it is less limited in spatial and temporal
 87 scope and resolution than weather stations or field observations (AghaKouchak et al., 2015).

88 To quantify the frequency of drought during different seasons across landscapes, we used the
 89 remotely sensed Vegetative Health Index (VHI), which measures landscape scale reductions
 90 in plant cover and temperature conditions characteristic of drought (Kogan, 2001).

91 Generated from data collected by NOAA AVHRR satellites since 1981, the VHI combines
 92 normalized difference vegetation index (NDVI) derived measures of vegetative stress
 93 (Vegetative Condition Index - VCI) with temperature stress indicated by anomalies in
 94 thermal spectra (Temperature Condition Index - TCI).

95 The VHI of year y during week w of [1, 52] at pixel i is derived from the following
 96 equations, where n is the number of years observed.

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

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

98 $NDVI_{max} = \max(NDVI_{1981,w,i}, \dots, NDVI_{1981+n,w,i})$

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

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

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

100 Thus, VHI measurements are standardized according to conditions historically
 101 observed at each locations. These measurements have been validated and generally used for
 102 evaluating drought risk and predicting crop yields in agriculture (e.g., Rojas, Vrieling, &
 103 Rembold, 2011; Kogan et al., 2016). But they also present a tool to study seasonal patterns
 104 in the frequency of drought across environments and to test hypotheses about the effect of
 105 drought on ecological and evolutionary processes. Indeed, the VHI has been applied recently
 106 to study drought related ecology of natural species and proven useful for predicting
 107 infraspecific variation in drought tolerance traits and genes (Dittberner et al., 2018; Mojica
 108 et al., 2016; Monroe et al., 2018). Here, we accessed VHI data at $16km^2$ resolution from 1981
 109 to 2015 (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) to characterize
 110 the seasonal drought frequencies experienced by annual and perennial *Heliophila* sepecies.

111 **Life history data for *Heliophila*.** *Heliophila* is a genus of flowering plants
 112 endemic to the southern portion of Africa including the Cape Floristic and Succulent Karoo
 113 Regions. These are among the most botanically diverse environments on Earth and the
 114 estimated ~50 *Heliophila* species are considered to be the most diverse genus of the family
 115 Brassicaceae (Mummenhoff, Al-Shehbaz, Bakker, Linder, & Mühlhausen, 2005). This genus
 116 includes both perennial and annual species and this change in life history strategy has likely
 117 arisen multiple independent times (Appel & Al-Shehbaz, 1997; Mummenhoff et al., 2005).
 118 We used life histories reported by Mummenhoff et al. (2005), grouping species with annual
 119 or perennial life histories. Perenniality was defined based on the traditional defition and

120 included any form of perennial life history (e.g., herbs, shrubs, mixed, etc).

121 **Heliophila herbarium specimens.** Botanists have collected and maintained over
122 350 million botanical specimens worldwide over the past 300 years. Herbarium specimens
123 and their associated metadata have been used since the 1960s to study species' geographical
124 distributions (reviewed by Willis et al. (2017) and Lang, Willems, Scheepens, Burbano, and
125 Bossdorf (2018)). And as they become digitized (Soltis, 2017), these collections have been
126 used to study relationships between trait distributions, geography, and climate (Davis, Willis,
127 Connolly, Kelly, & Ellison, 2015; Stropp et al., 2016; Václavík, Beckmann, Cord, &
128 Bindewald, 2017; Wolf, Zimmerman, Anderegg, Busby, & Christensen, 2016). To
129 characterize the diributions of annual and perennial *Heliophila* species, all records for the
130 genus *Heliophila* were downloaded from the Global Biodiversity Information Facility
131 (gbif.org) on July 21, 2018.

132 **Sequence data for phylogeny.** Aligned *Heliophila* ITS sequences were obtained
133 from previous work by Mandáková et al. (2012). *Aethionema*, *Alliaria*, *Cardamine*, *Chamira*,
134 and *Rorippa* ITS records from were downloaded from Genbank [] and aligned together with
135 *Heliophila* ITS sequences using MAFFT as outgroups [].

136 **Analyses**

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

144 the winter, spring, summer, and fall were extracted for the locations of all GBIF records.

145 **Herbarium record quality control.** To remove instance with spurious location

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

147 * Species with reported life history

148 * Records with geospatial data

149 * Records without known geospatial issues

150 * Records from collection sites classified as land pixels

151 * Records from Africa

152 * Non-duplicate records (ie. identical species, location, collection date)

153 **Phylogeny construction.** Model selection for construction of phylogeny was

154 performed in jModeltest2 with CIPRES (cite). Based on this analysis, *GTR + L* were

155 selected. Ultrametric phylogeny was estimated with branch lengths as relative time (details).

156 **Comparison of drought frequency between annual and perennial.** To

157 evaluate the hypothesis that annual and perennial life history strategies reflect adaptations

158 to alternative drought regimes, we tested the corresponding prediction that the observed

159 distributions of annual and perennial *Heliophila* species would be significantly associated

160 with historic drought frequency. The relationship between drought frequencies across each

161 taxon's range and life habitat (annual or perennial) was evaluated using Firth's

162 penalized-likelihood logistic regression and phylogenetic logistic regression.

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

164 escape drought prone seasons as seeds, collection dates for herbarium specimens were

165 compared between annual and perennial species. Comparisons of distributions were made by

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

167

Results

168 To test the hypothesis that annual and perennial plants reflect adaptation to
169 alternative drought environments we examined the landscape distribution of life history
170 strategies in the large and diverse mustard genus, *Heliophila* Figure 1. Using both herbarium
171 specimen metadata and a 30 year dataset of satellite generated climate information, we
172 tested the prediction that annual species are more often observed in drought-prone locations
173 than perennial species, when controlling for phylogenetic relatedness. We found that drought
174 frequency is significantly different between the distributions of annual and perennial species,
175 with annuals being found in environments with significantly more frequent drought, and that
176 this signal is strongest during the summer. These results remain significant while controlling
177 for the phylogenetic relationships of *Heliophila* species, yielding support for the role that
178 natural selection has played in driving contemporary distributions of these alternatives
179 strategies in relation to drought regimes.

180

GBIF records.

Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history (Mummenhoff et al., 2005), 3653 had geospatial data, 3627 did not have geospatial issues, 3460 were located on pixels classified as land having drought measurements, 3457 were located in Africa, 3162 were not duplicated. After all filtering steps, 2192 records for 42 species (Figure 2, Table S1) passed.

185

Drought frequency.

Drought frequency was significantly different between annual and perennial species.

187

Collection dates.

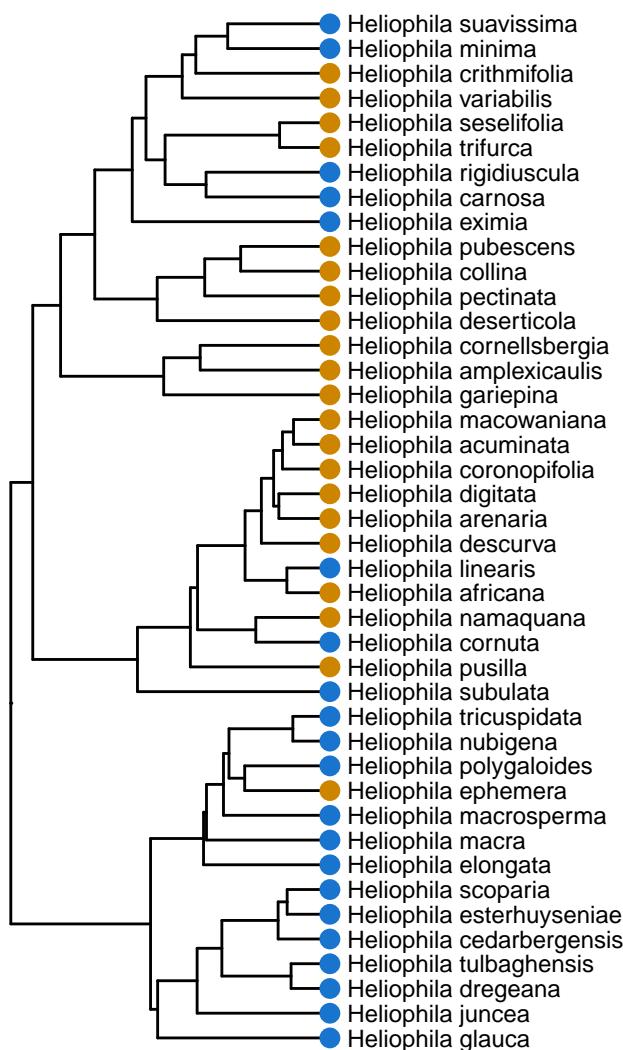
a

Figure 1. Phylogeny of *Heliophila*.

188

Discussion

189 **Summary**

190 We found that the distribution of annual and perennial species of *Heliophila* is
 191 significantly predicted by satellite detected historic drought frequencies. Annual species are
 192 found in environments that experience more frequent drought during the summer and fall

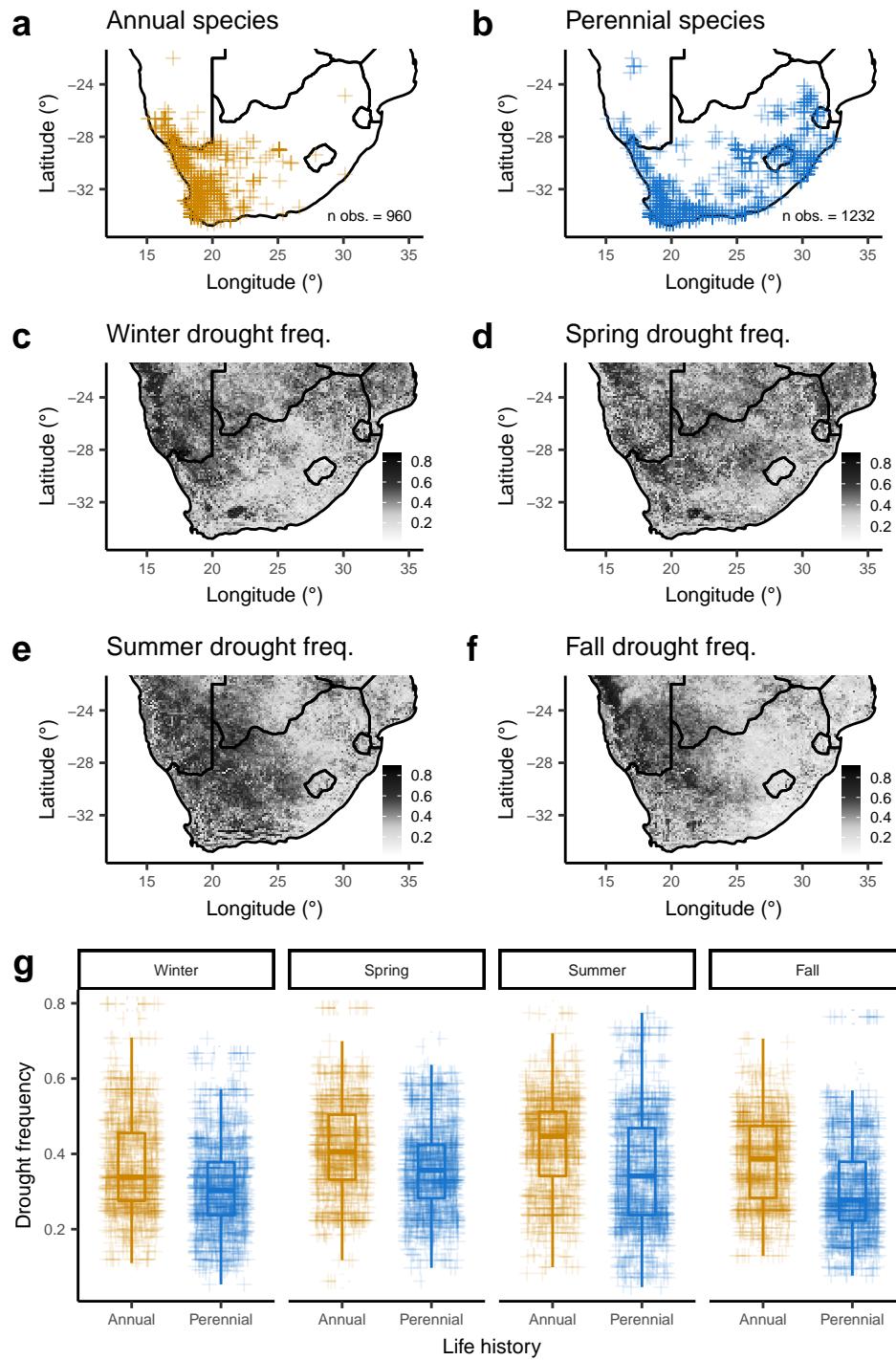


Figure 2. Locations of annual and perennial *Heliophila*. Drought frequency during the winter, spring, summer and fall. Drought frequencies during each season observed at the collection sites of *Heliophila* records.

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.

193 quarters compared to perennials. This relationship was consistent while controlling for
 194 phylogenetic relatedness among the taxa studied, indicating that these distributions cannot
 195 be explained entirely by common ancestry. These results support the hypothesis that natural
 196 selection has played a role in shaping the contemporary distributions of these alternative
 197 life-history strategies.

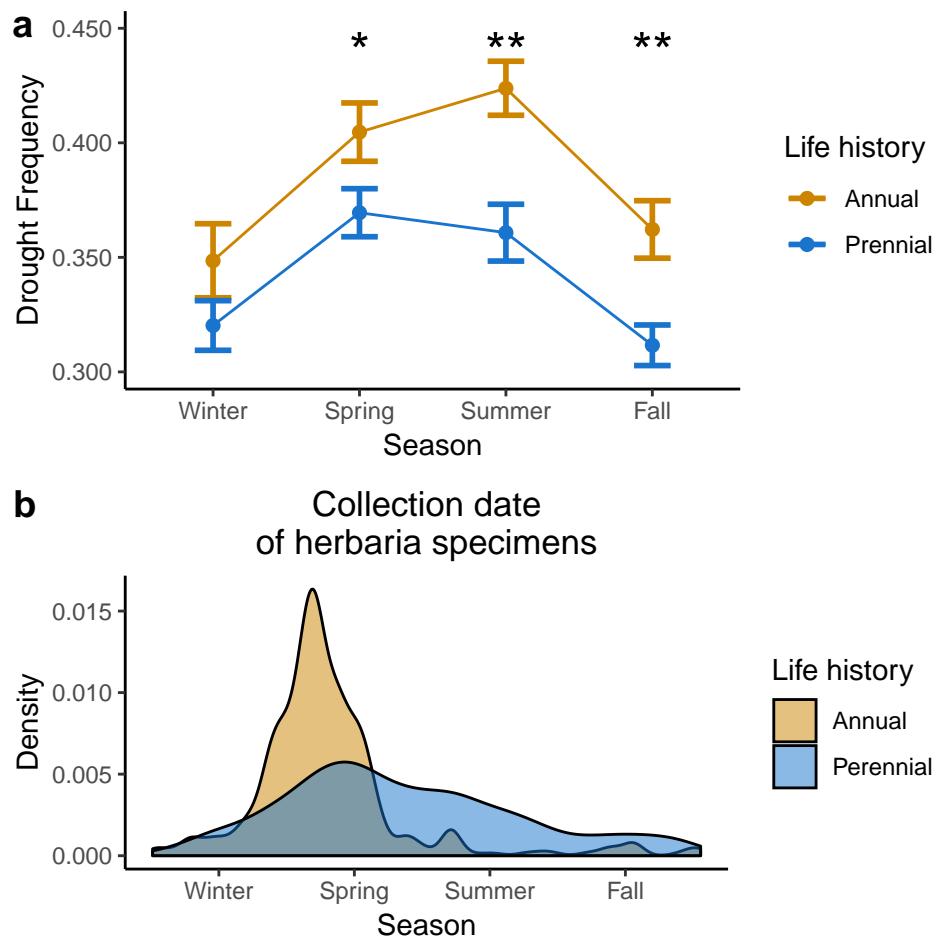


Figure 3. Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (B) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

¹⁹⁸ **Relationship to previous hypotheses/work**

¹⁹⁹ Herbaria records and satellite detected drought provide data with which the
²⁰⁰ distributions of annual and perennial species can be compared with respect to historic
²⁰¹ drought frequency. However, it is necessary to control for the demographic history caused by
²⁰² common ancestry of species if evolutionary processes such as natural selection are to be
²⁰³ invoked as explanations for any differences observed. If, for example, annual and perennial
²⁰⁴ species show significantly different ranges with respect to historic drought this could be

205 confounded by common ancestry if annuals originated from a common ancestor and vice
206 versa. In this case, it would be challenging to distinguish between natural selection and
207 demographic history. On the other hand, if annual and perennial life history strategies arose
208 independently in multiple species, controlling for phylogenetic relationships allows us to
209 better account for demography and make stronger assertions about the importance of
210 processes such as natural selection to explain patterns.

211 These findings support classical theoretical predictions about the adaptive value of
212 annual and perennial life history strategies. Taken together, they suggest that in *Heliophila*,
213 annual species are adapted to environments with increased summer droughts by avoiding
214 these seasons in a dormant seed phase of their life cycle. Indeed, we found that very few
215 annuals are collected during this season, supporting the prediction that they are not in a
216 vegetative and/or reproductive phase at this time. Traditionally, the focus has been on the
217 evolutionary origins of annual life histories {citations}. However, we also find evidence that
218 the transition to perenniability could be explained by historical drought regimes. The
219 phylogeny reveals several transitions from annual to perennial life history. Perennials may be
220 able to out compete annual relatives in environments where the infrequency of drought
221 favors strategies that allow plants to benefit from growth over many seasons.

222 **Caveats**

223 Sampling bias (Daru et al., 2018). Correlation does not prove causation. But it does
224 indicate predictive power and is consistent with adaptive hypotheses. Herbarium collections
225 and their associated data do not represent systematic or random sampling of a species
226 distribution. Significant biases in collecting exist, which we have not necessarily controlled for
227 here, and may have some effect on our findings, such as a bias toward collecting near roads
228 or near the locations of natural history collections (Daru et al. 2018, Heberling, in press).
229 Despite these biases, the Cape Floristic region is a biodiversity hotspot and one of the most

230 botanically well sampled regions on Earth (Daru et al. 2018, Heberling, in press?), suggesting
231 that this may currently be the optimal region for our analyses of life history distribution.
232 Future research will benefit from systematic sampling efforts to avoid these noted biases.
233 The climate data used here are assessed only from 198X-XXXX and do not reflect conditions
234 at the estimated divergence dates of these species (XXX million of years ago). Rather, the
235 results suggest that the current distributions of annual and perennial species reflect a history
236 of environmental filtration and ongoing natural selection. That is, their distributions are
237 non-random with respect to historic drought and this is not explained by phylogeny.

238 Broader implications

239 These findings suggest that rapidly changing drought regimes threaten species adapted
240 to current environments. Studies predict changing drought regimes. This could have impacts
241 on ecosystem functioning. This should also be considered when thinking about using
242 perennial crops. Studies predict changing drought regimes.

243 Do annuals require drought? We found independent origins of perenniability in
244 environments where droughts are infrequent. Annuals may not be able to compete with
245 perennials in the absence of droughts.

246 Conclusions

247 Perenniability appears to be adaptive in environments with less frequent drought. This
248 work demonstrates the power of emerging data to address outstanding classic hypotheses in
249 ecology and evolution.

250

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251

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252

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413

Supplement

414 **Software used.** We used R (Version 3.5.1; R Core Team, 2018) and the R-packages
 415 *ape* (Version 5.2; Paradis & Schliep, 2018; Orme et al., 2018; Soetaert, 2018), *bindrcpp*
 416 (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme et al., 2018), *coda* (Version 0.19.2;
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 418 (Version 0.7.8; Wickham et al., 2018), *forcats* (Version 0.3.0; Wickham, 2018a), *gee* (Version
 419 4.13.19; R by Thomas Lumley & author., 2015), *geiger* (Version 2.0.6; Alfaro et al., 2009;
 420 Eastman, Alfaro, Joyce, Hipp, & Harmon, 2011; Harmon, Weir, Brock, Glor, & Challenger,
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 422 Heinze & Ploner, 2018), *maps* (Version 3.3.0; Richard A. Becker, Ray Brownrigg.
 423 Enhancements by Thomas P Minka, & Deckmyn., 2018), *MASS* (Version 7.3.51.1; Venables
 424 & Ripley, 2002), *Matrix* (Version 1.2.15; Bates & Maechler, 2018), *MCMCglmm* (Version
 425 2.26; Hadfield, 2010), *mvtnorm* (Version 1.0.8; Genz & Bretz, 2009), *papaja* (Version
 426 0.1.0.9842; Aust & Barth, 2018), *phylolm* (Version 2.6; Ho & Ane, 2014), *phytools* (Version
 427 0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry & Wickham, 2018), *raster* (Version 2.8.4;
 428 Hijmans, 2018), *readr* (Version 1.2.1; Wickham et al., 2017), *shape* (Version 1.4.4; Soetaert,
 429 2018), *sp* (Version 1.3.1; Pebesma & Bivand, 2005), *stringr* (Version 1.3.1; Wickham, 2018b),
 430 *tibble* (Version 1.4.2; Müller & Wickham, 2018), *tidyverse* (Version 0.8.2; Wickham & Henry,
 431 2018), and *tidyverse* (Version 1.2.1; Wickham, 2017) for all our analyses.

432

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.