

<sup>1</sup> Drought frequency predicts plant life history strategies

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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

30 Drought frequency predicts plant life history strategies

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 which complete their seed to seed life cycle within a single  
37 calendar year from perennials which can persist over multiple years. Annual plants flower  
38 once, set seed, senesce, and then die, spending at least some portion of the year as a seed,  
39 where they are relatively protected from environmental stress. In contrast, perennial plants  
40 can continue vegetative growth after reproduction and must survive conditions experienced  
41 during all seasons. These represent fundamentally different life history strategies, but the  
42 ecological factors that explain their evolution and distributions remain empirically unresolved  
43 (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 & Gadgil, 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 *Oryza*  
55 *perennis* (Morishima, Sano, & Oka, 1984) and *Oenothera* (Evans, Hearn, Hahn, Spangle, &

56 Venable, 2005). Additionally, annual and perennial species of *Nemesia* were qualitatively  
57 associated with winter rather than summer rainfall environments respectively (Datson,  
58 Murray, & Steiner, 2008) and annual species of *Scorzonerooides* were associated with  
59 environments classified as unpredictable (Cruz-Mazo, Buide, Samuel, & Narbona, 2009).  
60 However, whether the history frequency of drought events indeed predicts the distributions  
61 annual or perennial life history strategies has yet to be tested in a phylogenetic context with  
62 suitable sample 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 history collections to test these classic hypotheses about the  
65 evolution of life history strategies within the African endemic mustard genus, *Heliophila* L.  
66 (Brassicaceae). If annuality is an adaptive strategy allowing plants to escape drought prone  
67 seasons, then drought frequency should predict the distribution of life history strategies  
68 across landscapes, and annual species should be more commonly associated with drought  
69 prone regions than perennial species. Furthermore, if annual species have adapted to escape  
70 drought prone seasons, observations of growing annual species (i.e. occurring in forms other  
71 than seed) should be rare during drought prone seasons. Phylogenetic relatedness can have  
72 significant non-random effects on species distributions and life history traits (Barrett,  
73 Harder, & Worley, 1996), and therefore we assessed the relationship between life history  
74 distribution and drought frequency in a phylogenetically 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>. Software  
79 used is listed in the supplement.

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

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

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

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

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

95        Thus, VHI measurements are standardized according to conditions historically  
 96 observed at each locations. These measurements have been validated and generally used for  
 97 evaluating drought risk and predicting crop yields in agriculture (e.g., Rojas, Vrieling, &  
 98 Rembold, 2011; Kogan et al., 2016). But they also present a new tool to study seasonal

99 patterns in the frequency of drought across environments and to test hypotheses about the  
100 effect of drought on ecological and evolutionary processes (Kerr & Ostrovsky, 2003). As such,  
101 the VHI has been applied recently to study drought related ecology of natural species and  
102 proven useful for predicting infraspecific variation in drought tolerance traits and genes  
103 (Dittberner et al., 2018; Mojica et al., 2016; Monroe et al., 2018). Here, we accessed VHI  
104 data at  $16\text{km}^2$  resolution from 1981 to 2015  
105 ([https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh\\_ftp.php](https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php)) to characterize the  
106 seasonal drought frequencies experienced by annual and perennial *Heliophila* species.

107 **Life history data for *Heliophila*.** *Heliophila* is a genus of flowering plants  
108 endemic to the southern portion of Africa including the Cape Floristic and Succulent Karoo  
109 Regions. These are among the most botanically diverse environments on Earth and the  
110 estimated ~50 *Heliophila* species occurring there are considered to make up the most diverse  
111 genus of the family Brassicaceae (Mandáková et al., 2012; Mummenhoff, Al-Shehbaz, Bakker,  
112 Linder, & Mühlhausen, 2005). This genus includes both perennial and annual species and  
113 this change in life history strategy has likely arisen multiple independent times (Appel &  
114 Al-Shehbaz, 1997; Mummenhoff et al., 2005). Furthermore, the fine scale climatic  
115 heterogeneity of Southern Africa is ideal for studying the distribution of traits in relation to  
116 environmental parameters (Sayre et al., 2013). We used life histories reported by  
117 Mummenhoff et al. (2005), grouping species with annual or perennial life histories.  
118 Perenniality was defined based any form of perennial life history (e.g., herbs, shrubs, mixed,  
119 etc). We also repeated these analyses without *H. subulata* and *H. minima* which have mixed  
120 life histories and found similar results. Because the original authors didn't report the nature  
121 of the mixed trait (Mummenhoff et al., 2005), (ie. plasticity vs. genetic variation), we  
122 classified these species here as perennial since they have the capacity to maintain vegetative  
123 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, 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.

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

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

- 149        • records for species with reported life history
- 150        • records with geospatial data
- 151        • records without known geospatial coordinate issues (i.e., coordinates reported are those  
152        of herbarium)
- 153        • records from collection sites classified as land pixels
- 154        • records from Africa (to exclude locations of cultivation)
- 155        • records without duplicates (i.e., identical species, location, collection date)

156        **Phylogeny construction.** Out group species were aligned together with *Heliphila*

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

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

159 phylogeny was estimated with branch lengths as relative time.

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

161 To evaluate the hypothesis that annual and perennial life history strategies reflect  
162 adaptations to alternative drought regimes, we tested the corresponding prediction that the  
163 observed distributions of annual and perennial *Heliphila* species would be significantly  
164 associated with historic drought frequency. First, we compared the frequency of drought  
165 during the winter, spring, summer, and fall between raw occurrence records of annual and  
166 perennial species by t-tests. To account for variation in the number of occurrence records per  
167 species, we next calculated the mean drought frequency during the winter, spring, summer  
168 and fall for each species. The relationships between species mean values of drought frequency  
169 during each season and life habitat (annual or perennial) were tested using Firth's  
170 penalized-likelihood logistic regressions. Because demographic histories caused by ancestry  
171 can confound trait - environment associations, we then tested for the relationships between  
172 drought frequency and life history while controlling for relationships between species using

173 phylogenetic logistic regressions.

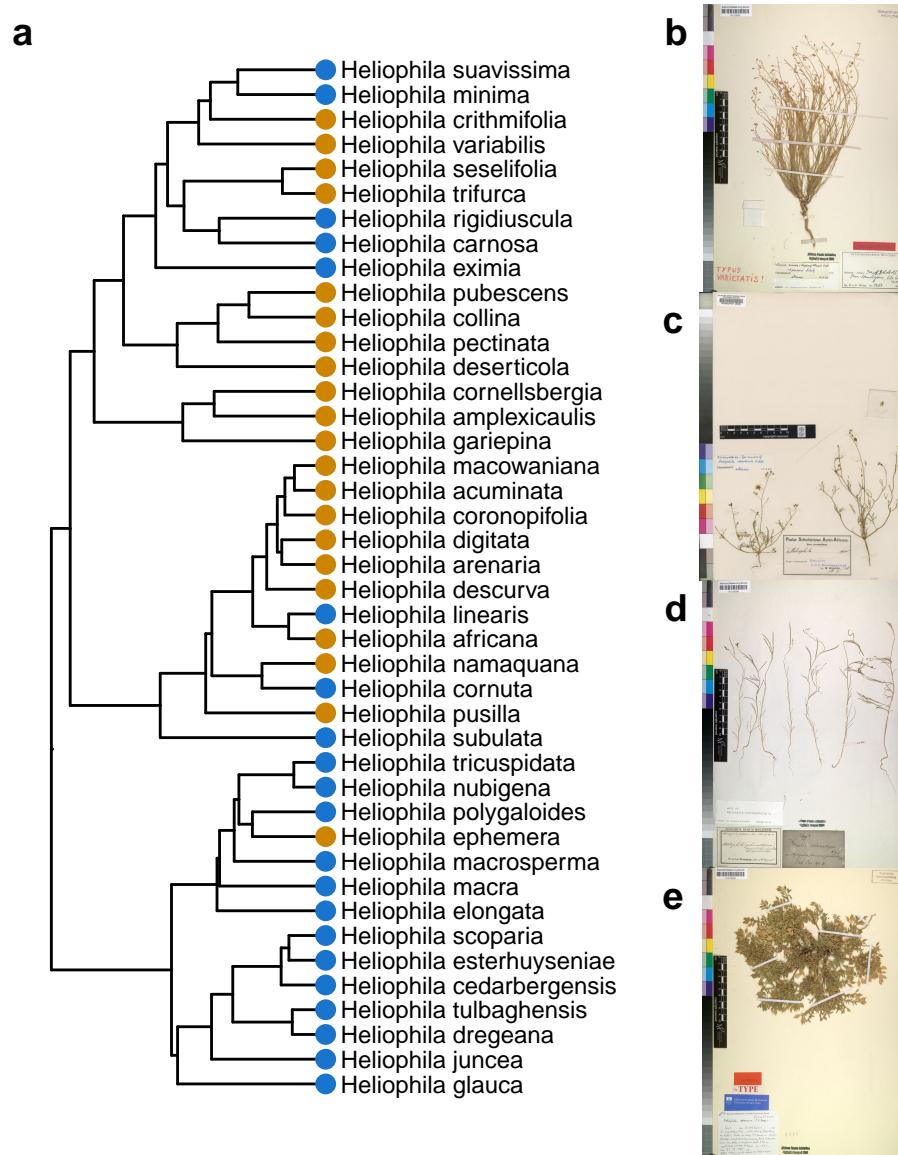
174 **Collection dates.** To test the hypothesis that annual species have adapted to  
175 escape drought prone seasons as seeds, collection dates for herbarium specimens were  
176 compared between annual and perennial species. Comparisons of distributions were made by  
177 Two-sample Kolmogorov-Smirnov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

178 **Results**

179 Out of 8670 *Heliphila* GBIF records, 6634 were for species with reported life history  
180 (Mummenhoff et al., 2005), 3653 had geospatial data, 3627 did not have geospatial issues,  
181 3460 were located on pixels classified as land having drought measurements, 3457 were  
182 located in Africa, 3162 were not duplicated. After all filtering steps, 2192 records for 42  
183 species (Figure 1, Table S1) passed for further analyses. The number of samples varied  
184 between species, with a mean of 52.19 samples per species. *Heliphila rigidiuscula* had the  
185 most records, 201, and *Heliphila cornellsbergia* the fewest, 2 (Table S1).

186 There were clear visual differences between the distributions of the 960 annual and the  
187 1232 perennial *Heliphila* observation records (see Figure S1 for maps of individual species).  
188 While annual species were generally found in the western regions of South Africa and  
189 Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the  
190 occurrences of perennials extended to the east coast of South Africa (Figure 2b).

191 The frequency of drought varied considerably across the ranges of *Heliphila* species  
192 (Figure 2c-f). This heterogeneity is expected, given that this is one of the most climatically  
193 diverse regions of the Earth (Sayre et al., 2013). It is worth noting the east to west cline in  
194 drought frequency observed during the summer, which distinguishes the high drought  
195 frequency of the Kalahari Sands and Namid Desert phytogeographic regions from the low  
196 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.

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

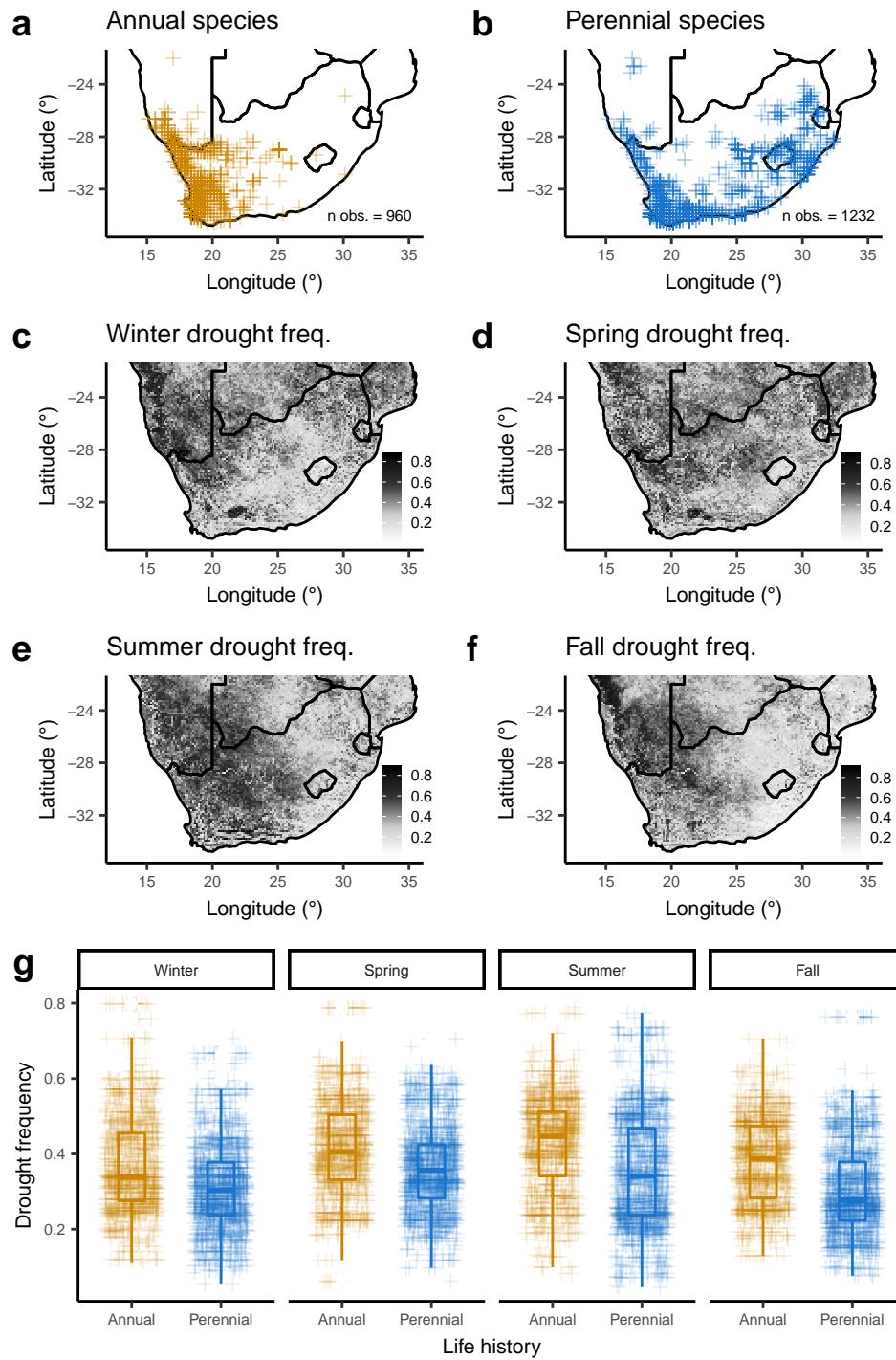


Figure 2. Locations of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall. (g) Drought frequencies during each season observed at the collection sites of *Heliophila* records.

Theory predicts 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 2g), 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

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.

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

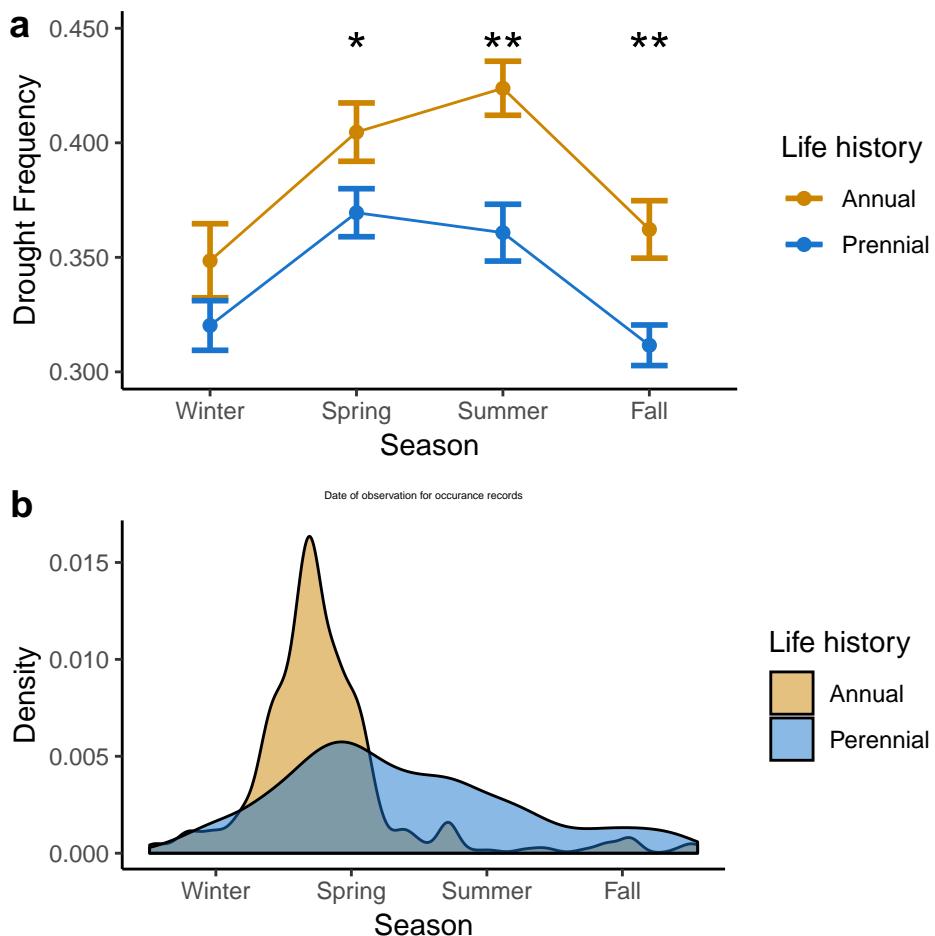


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (b) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

233

## Discussion

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

frequency is significantly different between the distributions of annual and perennial species, with annuals being found in environments with more frequent drought, and that this signal is strongest during the seasons when annuals are likely escaping via seed dormancy. These results remain significant while controlling for the phylogenetic relationships of *Heliophila* species, yielding support for the role that natural selection has played in driving contemporary distributions of these alternatives strategies in relation to drought regimens.

We cannot eliminate the possibility that confounding traits or environmental variables are the causative factors explaining variation in the distributions of annual and perennial species. Nevertheless, these results 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,

266 which represents a significant advance over relying on personal observations to characterize  
267 species distributions.

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

288 These findings suggest that species with locally adaptive life history strategies could be  
289 threatened by rapidly changing drought regimens (Dai, 2011). This could have impacts on  
290 ecosystem functioning and processes such as carbon cycling if the composition of annual and  
291 perennial species changes as a response [@garnier1997specific; Roumet, Urcelay, and Di'az

292 (2006);monroe2018ecoevolutionary]. Furthermore, the frequency of drought may be an  
293 important factor when considering the use of perennial cropping sysyems (Lelièvre & Volaire,  
294 2009; Parry, Flexas, & Medrano, 2005).

295 In conclusion, we find strong support for classic life history theory which predicts that  
296 annuality is adaptive in environments where droughts occur more frequently. Additionally,  
297 we report evidence consistent with a life history model in annuals in which they escape  
298 drought prone seasons during the seed phase of their life cycle. Finally, we find evidence that  
299 the distributions of perennial lineages may indicate a competitive advantage in areas where  
300 droughts are infrequent. More broadly, this work highlights the irreplaceable value of natural  
301 history collections and demonstrates the power of combining such information with large  
302 scale remote sensing data to address outstanding classic hypotheses in ecology and evolution.

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307 **References**

- 308 AghaKouchak, A., Farahmand, A., Melton, F., Teixeira, J., Anderson, M., Wardlow, B. D.,  
309 & Hain, C. (2015). Remote sensing of drought: Progress, challenges and  
310 opportunities. *Reviews of Geophysics*, 53(2), 452–480.
- 311 Alfaro, M., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D., ... Harmon, L.  
312 (2009). Nine exceptional radiations plus high turnover explain species diversity in  
313 jawed vertebrates. *Proceedings of the National Academy of Sciences of the United  
314 States of America*, 106, 13410–13414.
- 315 Andreasen, K., & Baldwin, B. G. (2001). Unequal evolutionary rates between annual and  
316 perennial lineages of checker mallows (*sidalcea*, malvaceae): Evidence from 18S–26S  
317 rDNA internal and external transcribed spacers. *Molecular Biology and Evolution*,  
318 18(6), 936–944.
- 319 Appel, O., & Al-Shehbaz, I. A. (1997). Generic limits and taxonomy of hornungia,  
320 pritzelago, and hymenolobus (brassicaceae). *Novon*, 338–340.
- 321 Aust, F., & Barth, M. (2018). *papaja: Create APA manuscripts with R Markdown*.  
322 Retrieved from <https://github.com/crsh/papaja>
- 323 Barrett, S. C. H., Harder, L. D., & Worley, A. C. (1996). The comparative biology of  
324 pollination and mating in flowering plants. *Phil. Trans. R. Soc. Lond. B*, 351(1345),  
325 1271–1280.
- 326 Bates, D., & Maechler, M. (2018). *Matrix: Sparse and dense matrix classes and methods*.  
327 Retrieved from <https://CRAN.R-project.org/package=Matrix>
- 328 Bena, G., Lejeune, B., Prosperi, J.-M., & Olivier, I. (1998). Molecular phylogenetic  
329 approach for studying life-history evolution: The ambiguous example of the genus  
330 *medicago* l. *Proceedings of the Royal Society of London B: Biological Sciences*,  
331 265(1401), 1141–1151.

- 332 Brown, P. M. (1996). OLDLIST: A database of maximum tree ages. *Tree Rings, Environment, and Humanity. Radiocarbon*, 1996, 727–731.
- 333
- 334 Charnov, E. L., & Schaffer, W. M. (1973). Life-history consequences of natural selection:
- 335 Cole's result revisited. *The American Naturalist*, 107(958), 791–793.
- 336 Cole, L. C. (1954). The population consequences of life history phenomena. *The Quarterly Review of Biology*, 29(2), 103–137.
- 337
- 338 Conti, E., Soltis, D. E., Hardig, T. M., & Schneider, J. (1999). Phylogenetic relationships of
- 339 the silver saxifrages (saxifraga, sect. Ligulatae haworth): Implications for the
- 340 evolution of substrate specificity, life histories, and biogeography. *Molecular Phylogenetics and Evolution*, 13(3), 536–555.
- 341
- 342 Corbin, J. D., & D'Antonio, C. M. (2004). Competition between native perennial and exotic
- 343 annual grasses: Implications for an historical invasion. *Ecology*, 85(5), 1273–1283.
- 344 Cruz-Mazo, G., Buide, M., Samuel, R., & Narbona, E. (2009). Molecular phylogeny of
- 345 scorzoneroideae (asteraceae): Evolution of heterocarpy and annual habit in
- 346 unpredictable environments. *Molecular Phylogenetics and Evolution*, 53(3), 835–847.
- 347
- 348 Dai, A. (2011). Drought under global warming: A review. *Wiley Interdisciplinary Reviews: Climate Change*, 2(1), 45–65.
- 349
- 350 Daru, B. H., Park, D. S., Primack, R. B., Willis, C. G., Barrington, D. S., Whitfeld, T. J., ...
- 351 others. (2018). Widespread sampling biases in herbaria revealed from large-scale digitization. *New Phytologist*, 217(2), 939–955.
- 352
- 353 Datson, P., Murray, B., & Steiner, K. (2008). Climate and the evolution of annual/perennial
- 354 life-histories in nemesia (scrophulariaceae). *Plant Systematics and Evolution*, 270(1-2), 39–57.

- 355 Davis, C. C., Willis, C. G., Connolly, B., Kelly, C., & Ellison, A. M. (2015). Herbarium  
356 records are reliable sources of phenological change driven by climate and provide  
357 novel insights into species' phenological cueing mechanisms. *American Journal of*  
358 *Botany*, 102(10), 1599–1609.
- 359 Dittberner, H., Korte, A., Mettler-Altmann, T., Weber, A., Monroe, G., & Meaux, J. de.  
360 (2018). Natural variation in stomata size contributes to the local adaptation of  
361 water-use efficiency in *arabidopsis thaliana*. *bioRxiv*, 253021.
- 362 Eastman, J., Alfaro, M., Joyce, P., Hipp, A., & Harmon, L. (2011). A novel comparative  
363 method for identifying shifts in the rate of character evolution on trees. *Evolution*, 65,  
364 3578–3589.
- 365 Evans, M. E., Hearn, D. J., Hahn, W. J., Spangle, J. M., & Venable, D. L. (2005). Climate  
366 and life-history evolution in evening primroses (oenothera, onagraceae): A  
367 phylogenetic comparative analysis. *Evolution*, 59(9), 1914–1927.
- 368 Franco, M., & Silvertown, J. (1996). Life history variation in plants: An exploration of the  
369 fast-slow continuum hypothesis. *Phil. Trans. R. Soc. Lond. B*, 351(1345),  
370 1341–1348.
- 371 Friedman, J., & Rubin, M. J. (2015). All in good time: Understanding annual and perennial  
372 strategies in plants. *American Journal of Botany*, 102(4), 497–499.
- 373 GBIF. (2018, July). GBIF occurrence download. Retrieved from  
374 <https://doi.org/10.15468/dl.xmwqxm>
- 375 Genz, A., & Bretz, F. (2009). *Computation of multivariate normal and t probabilities*.  
376 Heidelberg: Springer-Verlag.

- 377 Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models:  
378       The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22. Retrieved  
379       from <http://www.jstatsoft.org/v33/i02/>
- 380 Harmon, L., Weir, J., Brock, C., Glor, R., & Challenger, W. (2008). GEIGER: Investigating  
381       evolutionary radiations. *Bioinformatics*, 24, 129–131.
- 382 Heinze, G., & Ploner, M. (2018). *Logistf: Firth's bias-reduced logistic regression*. Retrieved  
383       from <https://CRAN.R-project.org/package=logistf>
- 384 Henry, L., & Wickham, H. (2018). *Purrrr: Functional programming tools*. Retrieved from  
385       <https://CRAN.R-project.org/package=purrr>
- 386 Hijmans, R. J. (2018). *Raster: Geographic data analysis and modeling*. Retrieved from  
387       <https://CRAN.R-project.org/package=raster>
- 388 Ho, L. S. T., & Ane, C. (2014). A linear-time algorithm for gaussian and non-gaussian trait  
389       evolution models. *Systematic Biology*, 63, 397–408.
- 390 Kerr, J. T., & Ostrovsky, M. (2003). From space to species: Ecological applications for  
391       remote sensing. *Trends in Ecology & Evolution*, 18(6), 299–305.
- 392 Kogan, F., Guo, W., Strashnaia, A., Kleshenko, A., Chub, O., & Virchenko, O. (2016).  
393       Modelling and prediction of crop losses from noaa polar-orbiting operational satellites.  
394       *Geomatics, Natural Hazards and Risk*, 7(3), 886–900.
- 395 Kogan, F. N. (2001). Operational space technology for global vegetation assessment.  
396       *Bulletin of the American Meteorological Society*, 82(9), 1949–1964.
- 397 Lang, P. L., Willems, F. M., Scheepens, J., Burbano, H. A., & Bossdorf, O. (2018). *Using  
398       herbaria to study global environmental change*. PeerJ Preprints.

- 399 Lelièvre, F., & Volaire, F. (2009). Current and potential development of perennial grasses in  
400 rainfed mediterranean farming systems. *Crop Science*, 49(6), 2371–2378.
- 401 Mandáková, T., Mummenhoff, K., Al-Shehbaz, I. A., Mucina, L., Mühlhausen, A., & Lysak,  
402 M. A. (2012). Whole-genome triplication and species radiation in the southern  
403 african tribe heliophileae (brassicaceae). *Taxon*, 61(5), 989–1000.
- 404 Mojica, J. P., Mullen, J., Lovell, J. T., Monroe, J. G., Paul, J. R., Oakley, C. G., & McKay,  
405 J. K. (2016). Genetics of water use physiology in locally adapted *Arabidopsis*  
406 *thaliana*. *Plant Science*. doi:10.1016/j.plantsci.2016.03.015
- 407 Monroe, J. G., Powell, T., Price, N., Mullen, J., Howard, A., Evans, K., ... McKay, J.  
408 (2018). Drought adaptation in nature by extensive genetic loss-of-function. *bioRxiv*,  
409 372854.
- 410 Morishima, H., Sano, Y., & Oka, H. (1984). Differentiation of perennial and annual types  
411 due to habitat conditions in the wild rice *Oryza perennis*. *Plant Systematics and*  
412 *Evolution*, 144(2), 119–135.
- 413 Mummenhoff, K., Al-Shehbaz, I. A., Bakker, F. T., Linder, H. P., & Mühlhausen, A. (2005).  
414 Phylogeny, morphological evolution, and speciation of endemic brassicaceae genera in  
415 the cape flora of southern africa. *Annals of the Missouri Botanical Garden*, 400–424.
- 416 Müller, K. (2018). *Bindrcpp: An 'rcpp' interface to active bindings*. Retrieved from  
417 <https://CRAN.R-project.org/package=bindrcpp>
- 418 Müller, K., & Wickham, H. (2018). *Tibble: Simple data frames*. Retrieved from  
419 <https://CRAN.R-project.org/package=tibble>
- 420 Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018).  
421 *Caper: Comparative analyses of phylogenetics and evolution in r*. Retrieved from

- 422 <https://CRAN.R-project.org/package=caper>
- 423 Paradis, E., & Schliep, K. (2018). Ape 5.0: An environment for modern phylogenetics and  
424 evolutionary analyses in R. *Bioinformatics*, *xx*, xxx–xxx.
- 425 Parry, M., Flexas, J., & Medrano, H. (2005). Prospects for crop production under drought:  
426 Research priorities and future directions. *Annals of Applied Biology*, *147*(3), 211–226.
- 427 Pebesma, E. J., & Bivand, R. S. (2005). Classes and methods for spatial data in R. *R News*,  
428 *5*(2), 9–13. Retrieved from <https://CRAN.R-project.org/doc/Rnews/>
- 429 Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and  
430 output analysis for mcmc. *R News*, *6*(1), 7–11. Retrieved from  
431 <https://journal.r-project.org/archive/>
- 432 R by Thomas Lumley, V. J. C. P. to, & author., B. R. N. that maintainers are not available  
433 to give advice on using a package they did not. (2015). *Gee: Generalized estimation*  
434 *equation solver*. Retrieved from <https://CRAN.R-project.org/package=gee>
- 435 R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna,  
436 Austria: R Foundation for Statistical Computing. Retrieved from  
437 <https://www.R-project.org/>
- 438 Revell, L. J. (2012). Phytools: An r package for phylogenetic comparative biology (and other  
439 things). *Methods in Ecology and Evolution*, *3*, 217–223.
- 440 Richard A. Becker, O. S. code by, Ray Brownrigg. Enhancements by Thomas P Minka, A. R.  
441 W. R. version by, & Deckmyn., A. (2018). *Maps: Draw geographical maps*. Retrieved  
442 from <https://CRAN.R-project.org/package=maps>
- 443 Rojas, O., Vrieling, A., & Rembold, F. (2011). Assessing drought probability for agricultural  
444 areas in africa with coarse resolution remote sensing imagery. *Remote Sensing of*

- 445       *Environment*, 115(2), 343–352.
- 446   Roumet, C., Urcelay, C., & Di'az, S. (2006). Suites of root traits differ between annual and  
447       perennial species growing in the field. *New Phytologist*, 170(2), 357–368.
- 448   Sayre, R. G., Comer, P., Hak, J., Josse, C., Bow, J., Warner, H., ... others. (2013). A new  
449       map of standardized terrestrial ecosystems of africa. *African Geographical Review*.
- 450   Schaffer, W., & Gadgil, M. (1975). Selection for optimal life histories in plants. *Ecology and  
451       Evolution of Communities.*, 142–157.
- 452   Slater, G., Harmon, L., Wegmann, D., Joyce, P., Revell, L., & Alfaro, M. (2012). Fitting  
453       models of continuous trait evolution to incompletely sampled comparative data using  
454       approximate bayesian computation. *Evolution*, 66, 752–762.
- 455   Soetaert, K. (2017). *Diagram: Functions for visualising simple graphs (networks), plotting  
456       flow diagrams*. Retrieved from <https://CRAN.R-project.org/package=diagram>
- 457   Soetaert, K. (2018). *Shape: Functions for plotting graphical shapes, colors*. Retrieved from  
458       <https://CRAN.R-project.org/package=shape>
- 459   Soltis, P. S. (2017). Digitization of herbaria enables novel research. *American Journal of  
460       Botany*, 104(9), 1281–1284.
- 461   Stearns, S. C. (1992). *The evolution of life histories*.
- 462   Stropp, J., Ladle, R. J., M. Malhado, A. C., Hortal, J., Gaffuri, J., H. Temperley, W., ...  
463       Mayaux, P. (2016). Mapping ignorance: 300 years of collecting flowering plants in  
464       africa. *Global Ecology and Biogeography*, 25(9), 1085–1096.
- 465   Tank, D. C., & Olmstead, R. G. (2008). From annuals to perennials: Phylogeny of subtribe  
466       castillejinae (orobanchaceae). *American Journal of Botany*, 95(5), 608–625.

- 467 Václaví'k, T., Beckmann, M., Cord, A. F., & Bindewald, A. M. (2017). Effects of uv-b  
468 radiation on leaf hair traits of invasive plants—combining historical herbarium  
469 records with novel remote sensing data. *PloS One*, 12(4), e0175671.
- 470 Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with s* (Fourth.). New  
471 York: Springer. Retrieved from <http://www.stats.ox.ac.uk/pub/MASS4>
- 472 Verboom, G. A., Linder, H. P., & Stock, W. D. (2004). Testing the adaptive nature of  
473 radiation: Growth form and life history divergence in the african grass genus ehrharta  
474 (poaceae: Ehrhartoideae). *American Journal of Botany*, 91(9), 1364–1370.
- 475 Wickham, H. (2016). *Ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.  
476 Retrieved from <http://ggplot2.org>
- 477 Wickham, H. (2017). *Tidyverse: Easily install and load the 'tidyverse'*. Retrieved from  
478 <https://CRAN.R-project.org/package=tidyverse>
- 479 Wickham, H. (2018a). *Forcats: Tools for working with categorical variables (factors)*.  
480 Retrieved from <https://CRAN.R-project.org/package=forcats>
- 481 Wickham, H. (2018b). *Stringr: Simple, consistent wrappers for common string operations*.  
482 Retrieved from <https://CRAN.R-project.org/package=stringr>
- 483 Wickham, H., François, R., Henry, L., & Müller, K. (2018). *Dplyr: A grammar of data  
484 manipulation*. Retrieved from <https://CRAN.R-project.org/package=dplyr>
- 485 Wickham, H., & Henry, L. (2018). *Tidyr: Easily tidy data with 'spread()' and 'gather()'  
486 functions*. Retrieved from <https://CRAN.R-project.org/package=tidyr>
- 487 Wickham, H., Hester, J., & Francois, R. (2017). *Readr: Read rectangular text data*.  
488 Retrieved from <https://CRAN.R-project.org/package=readr>

- 489 Willis, C. G., Ellwood, E. R., Primack, R. B., Davis, C. C., Pearson, K. D., Gallinat, A. S.,  
490 ... others. (2017). Old plants, new tricks: Phenological research using herbarium  
491 specimens. *Trends in Ecology & Evolution*, 32(7), 531–546.
- 492 Wolf, A., Zimmerman, N. B., Anderegg, W. R., Busby, P. E., & Christensen, J. (2016).  
493 Altitudinal shifts of the native and introduced flora of California in the context of  
494 20th-century warming. *Global Ecology and Biogeography*, 25(4), 418–429.

495

## Supplement

496       **Images used.** <https://www.gbif.org/occurrence/1099023487>  
497       <https://www.gbif.org/occurrence/1057389408> <https://www.gbif.org/occurrence/1099023562>  
498       <https://www.gbif.org/occurrence/1099023490>

499       **Software used.** We used R (Version 3.5.1; R Core Team, 2018) and the R-packages  
500       *ape* (Version 5.2; Paradis & Schliep, 2018; Orme et al., 2018; Soetaert, 2018), *bindrcpp*  
501       (Version 0.2.2; Müller, 2018), *caper* (Version 1.0.1; Orme et al., 2018), *coda* (Version 0.19.2;  
502       Plummer, Best, Cowles, & Vines, 2006), *diagram* (Version 1.6.4; Soetaert, 2017), *dplyr*  
503       (Version 0.7.8; Wickham et al., 2018), *forcats* (Version 0.3.0; Wickham, 2018a), *gee* (Version  
504       4.13.19; R by Thomas Lumley & author., 2015), *geiger* (Version 2.0.6; Alfaro et al., 2009;  
505       Eastman, Alfaro, Joyce, Hipp, & Harmon, 2011; Harmon, Weir, Brock, Glor, & Challenger,  
506       2008; Slater et al., 2012), *ggplot2* (Version 3.1.0; Wickham, 2016), *logistf* (Version 1.23;  
507       Heinze & Ploner, 2018), *maps* (Version 3.3.0; Richard A. Becker, Ray Brownrigg.  
508       Enhancements by Thomas P Minka, & Deckmyn., 2018), *MASS* (Version 7.3.51.1; Venables  
509       & Ripley, 2002), *Matrix* (Version 1.2.15; Bates & Maechler, 2018), *MCMCglmm* (Version  
510       2.26; Hadfield, 2010), *mvtnorm* (Version 1.0.8; Genz & Bretz, 2009), *papaja* (Version  
511       0.1.0.9842; Aust & Barth, 2018), *phylolm* (Version 2.6; Ho & Ane, 2014), *phytools* (Version  
512       0.6.60; Revell, 2012), *purrr* (Version 0.2.5; Henry & Wickham, 2018), *raster* (Version 2.8.4;  
513       Hijmans, 2018), *readr* (Version 1.2.1; Wickham et al., 2017), *shape* (Version 1.4.4; Soetaert,  
514       2018), *sp* (Version 1.3.1; Pebesma & Bivand, 2005), *stringr* (Version 1.3.1; Wickham, 2018b),  
515       *tibble* (Version 1.4.2; Müller & Wickham, 2018), *tidyverse* (Version 0.8.2; Wickham & Henry,  
516       2018), and *tidyverse* (Version 1.2.1; Wickham, 2017) for all our analyses.

517

## Supplementary tables and figures.

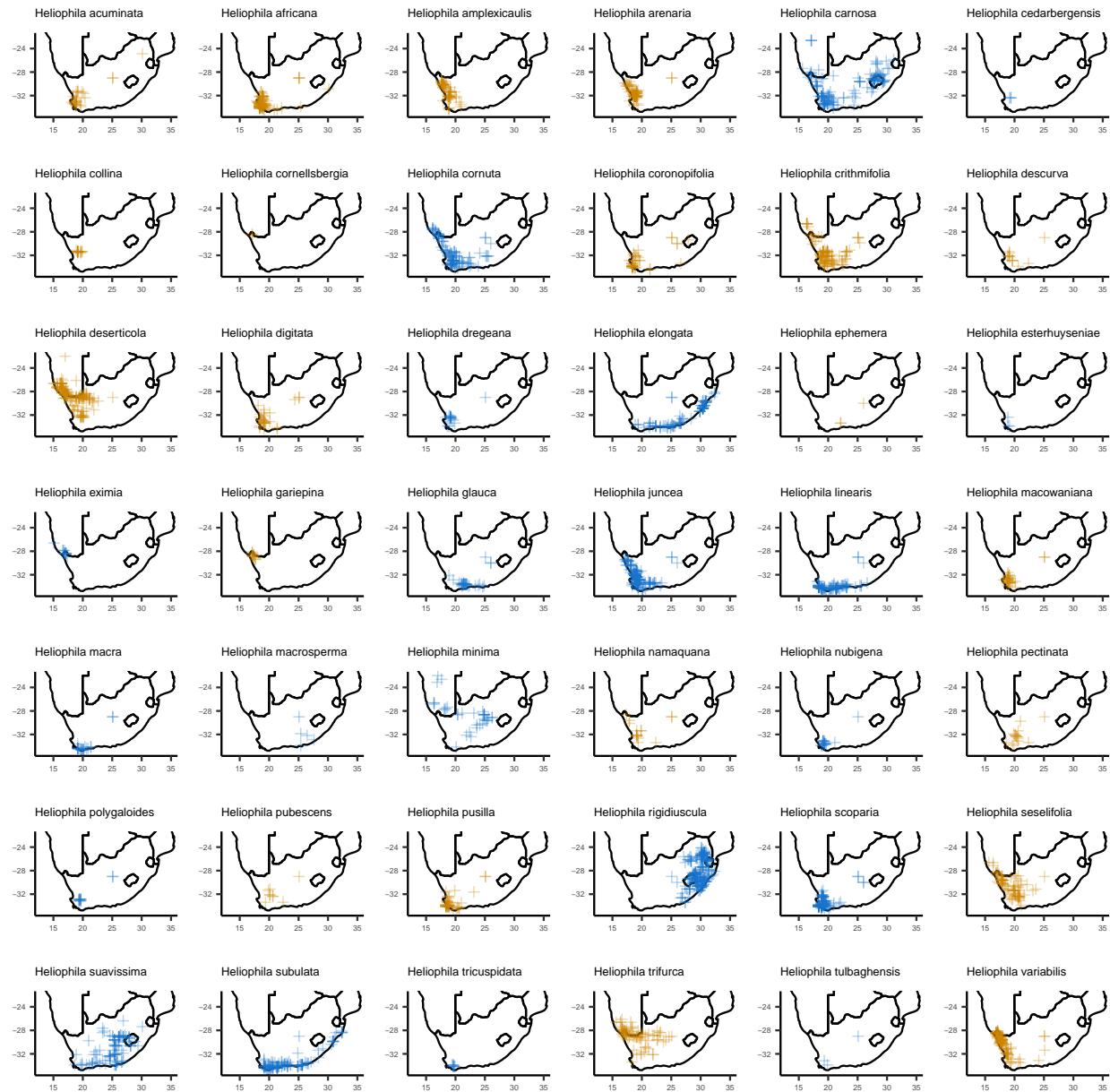
Table S1

*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.