

¹ Drought frequency predicts life history strategies in *Heliophila*

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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 stress events such as drought. Here we test this
15 hypothesis in *Heliophila* (Brassicaceae), a diverse genus of flowering plants native to Africa,
16 by integrating 34 years of satellite-based drought measurements with 2192 herbaria
17 occurrence records. 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 collection dates of annual
22 and perennial species indicate that annuals escape drought prone seasons during the seed
23 phase of their life cycle. Together, these findings provide empirical support for classic
24 hypotheses about the drivers of life history strategy in plants - that perennials out compete
25 annuals in environments with less frequent drought and that annuals are adapted to
26 environments with more frequent drought by escaping drought prone seasons as seeds.

27

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

29 Drought frequency predicts life history strategies in *Heliophila*

30 **Introduction**

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

43 Classical theory predicts shorter life spans in environments where adult mortality is
44 high (Charnov & Schaffer, 1973; Stearns, 1992; Franco & Silvertown, 1996). In plants, this
45 has been extended to the hypothesis that annuality is adaptive when it allows plants to
46 escape drought (Schaffer & Gadgil, 1975). Lack of water is perhaps the greatest threat to
47 survival during vegetative or reproductive growth and annuals can remain dormant (and
48 protected as a seed) during drought. Thus, environments with greater seasonal drought
49 frequency may select for annual life histories that complete reproduction prior to drought
50 prone seasons. Conversely, environments with less frequent drought may select for perennial
51 species, which benefit from multiple bouts of reproduction and competitive advantage by
52 preventing recruitment of annual species (Corbin & D'Antonio, 2004). These predictions
53 have been supported by the observation of annuals in arid environments in *Oryza perennis*
54 (Morishima *et al.*, 1984) and *Oenothera* (Evans *et al.*, 2005). Additionally, annual and

55 perennial species of *Nemesia* were qualitatively associated with winter rather and summer
56 rainfall environments respectively (Datson *et al.*, 2008) and annual species of *Scorzonerooides*
57 were associated with environments classified as unpredictable (Cruz-Mazo *et al.*, 2009).
58 However, whether the history frequency of drought events indeed predicts the distributions
59 annual or perennial life history strategies has yet to be tested.

60 Here we combine a long-term global dataset of satellite detected drought events with
61 metadata from natural history collections to test these classic hypotheses within the African
62 endemic mustard genus, *Heliphila* L. (Brassicaceae). If annuality is an adaptive strategy
63 allowing plants to escape drought prone seasons, then drought frequency should predict the
64 distribution of life history strategies across landscapes, and annual species should be more
65 commonly associated with drought prone regions than perennial species. Furthermore, if
66 annual species have adapted to escape drought prone seasons, observations of growing annual
67 species (i.e. occurring in forms other than seed) should be rare during drought prone seasons.
68 Phylogenetic relatedness can influence tests of associations between species' traits and their
69 environments (Felsenstein, 1985; Barrett *et al.*, 1996), and therefore we assessed the
70 relationship between life history distribution and drought frequency in a phylogenetic
71 context.

72 Materials and Methods

73 Data

74 **Availability.** All analyses were performed using R. All data and the source code to
75 produce this manuscript are available at <https://github.com/greymonroe/heliophila>.
76 Software used is listed in the supplement.

77 **Satellite-detected drought data.** Remotely sensed data is a powerful tool for
78 characterizing seasonal patterns in drought because it is less limited in spatial and temporal

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

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

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

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

89 where $NDVI_{min} = min(NDVI_{1981,w,i} \dots NDVI_{1981+n,w,i})$ and
 90 $NDVI_{max} = max(NDVI_{1981,w,i} \dots NDVI_{1981+n,w,i})$ and $T_{min} = min(T_{1981,w,i} \dots T_{1981+n,w,i})$
 91 and $T_{max} = max(T_{1981,w,i} \dots T_{1981+n,w,i})$

92 Thus, VHI measurements are standardized according to conditions historically
 93 observed at each locations. These measurements have been validated and generally used for
 94 evaluating drought risk and predicting crop yields in agriculture (e.g., Rojas *et al.*, 2011;
 95 Kogan *et al.*, 2016). But they also present a new tool to study seasonal patterns in the
 96 frequency of drought across environments and to test hypotheses about the effect of drought
 97 on ecological and evolutionary processes (Kerr & Ostrovsky, 2003). As such, the VHI has

been applied recently to study drought related ecology of natural species and proven useful for predicting intraspecific variation in drought tolerance traits and genes (Mojica *et al.*, 2016; Dittberner *et al.*, 2018; Monroe *et al.*, 2018b). Here, we accessed VHI data at 16km² resolution from 1981 to 2015 (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) to characterize the seasonal drought frequencies experienced by annual and perennial *Heliophila* species.

Life history data for *Heliophila*. *Heliophila* is a genus of flowering plants endemic to the southern portion of Africa including the Cape Floristic and Succulent Karoo Regions. These are among the most botanically diverse environments on Earth and the *Heliophila* species occurring there are considered to make up the most diverse genus of the family Brassicaceae (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). This genus includes both perennial and annual species and this change in life history strategy has likely arisen multiple independent times (Appel & Al-Shehbaz, 1997; Mummenhoff *et al.*, 2005). Furthermore, the fine scale climatic heterogeneity of Southern Africa is ideal for studying the distribution of traits in relation to environmental parameters (Sayre *et al.*, 2013). We used life histories reported by Mummenhoff *et al.* (2005), grouping species with annual or perennial life histories. Perenniality was defined based any form of perennial life history (e.g., herbs, shrubs, mixed, etc). Because the nature of species reported with mixed traits were unknown (i.e. plasticity vs. genetic variation), we classified these species here as perennial since they can maintain vegetative growth after reproduction at least to some capacity.

***Heliophila* occurrence records.** Botanists have collected and maintained over 350 million botanical specimens worldwide over the past 300 years (Thiers, 2016). 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 *et al.* (2018)). And as they become digitized (Soltis, 2017), these collections have been used to study relationships between trait distributions, geography, and climate (Davis *et al.*, 2015; Stropp *et al.*, 2016;

¹²⁴ Wolf *et al.*, 2016; Václavík *et al.*, 2017). To characterize the distributions of annual and
¹²⁵ perennial *Heliphila* species, all records for the genus *Heliphila* were downloaded from the
¹²⁶ Global Biodiversity Information Facility (gbif.org) on July 21, 2018 (GBIF, 2018).

¹²⁷ **Sequence data for phylogeny.** An alignment of ITS I and II sequences for
¹²⁸ *Heliphila* species was obtained from the authors of Mandáková *et al.* (2012). Individual ITS
¹²⁹ I and II sequences for *Aethionema grandiflorum*, *Alliaria petiolata*, *Cardamine matthioli*,
¹³⁰ *Chamira circaeoides*, and *Rorippa amphibia* were downloaded from Genbank.

¹³¹ **Analyses**

¹³² **Drought frequency calculations.** To characterize drought regimens across the
¹³³ distributions of annual and perennial species of *Heliphila*, we calculated drought during
¹³⁴ different seasons at the location of observations for *Heliphila* records using the VHI.
¹³⁵ Specifically, we created global maps of the frequencies of observing drought conditions
¹³⁶ (VHI<40, NOAA) during the winter (quarter surrounding winter solstice), spring (quarter
¹³⁷ surrounding spring equinox), summer (quarter surrounding summer solstice) and fall (quarter
¹³⁸ surrounding fall equinox) from 1981 to 2015. From these maps, the drought frequency during
¹³⁹ the winter, spring, summer, and fall were extracted for the locations of all GBIF records.

¹⁴⁰ **Filtering of occurrence records.** To avoid instances with spurious location data,
¹⁴¹ we filtered raw GBIF by restricting our analyses to include only:

- ¹⁴² • records for species with reported life history
- ¹⁴³ • records with geospatial data
- ¹⁴⁴ • records without known geospatial coordinate issues (i.e., coordinates reported are those
of herbarium)
- ¹⁴⁶ • records from collection sites classified as land pixels in the VHI dataset
- ¹⁴⁷ • records from Africa (to exclude locations of cultivation)

- 148 • records without duplicates (i.e., identical species, location, collection date)

149 **Phylogeny construction.** Out group (*Aethionema grandiflorum*, *Alliaria petiolata*,
150 *Cardamine matthioli*, *Chamira circaeoides*, and *Rorippa amphibia*) and ingroup *Helophil*
151 ITS I and II sequences were aligned using MAFFT (Katoh *et al.*, 2002) with strategy
152 G-INS-I, offset value 0.1, and all other options set as default. The *GTR + Γ* model of
153 nucleotide substitution was determined to best fit the data based on AIC using jModelTest2
154 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012). A maximum clade credibility tree with
155 branch lengths as relative time was estimated by summarizing data from six runs of
156 100,000,000 generations of Bayesian Markov chain Monte Carlo conducted in BEAST 2
157 (Bouckaert *et al.*, 2014). Model selection and phylogenetic analyses were conducted through
158 the CIPRES Science Gateway (Miller *et al.*, 2010).

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

160 To evaluate the hypothesis that annual and perennial life history strategies reflect
161 adaptations to alternative drought regimes, we tested the corresponding prediction that the
162 observed distributions of annual and perennial *Helophil* species would be significantly
163 associated with historic drought frequency. First, we compared the frequency of drought
164 during the winter, spring, summer, and fall between total occurrence records of annual and
165 perennial species by t-tests. To account for variation in the number of occurrence records per
166 species, we next calculated the mean drought frequency during the winter, spring, summer
167 and fall for each species. Because shared evolutionary history of closely related species can
168 lead to spurious associations between traits and environments (Felsenstein, 1985), we tested
169 for a relationship between life history strategy and drought frequency while controlling for
170 phylogeny using phylogenetic logistic regression (Ives & Garland, 2010).

171 **Collection dates.** To test the hypothesis that annual species have adapted to
172 escape drought prone seasons as seeds, collection dates for herbarium specimens were
173 compared between annual and perennial species. Comparisons of distributions were made by

¹⁷⁴ Two-sample Kolmogorov-Smirnov test and Barlett variance test.

¹⁷⁵

Results

¹⁷⁶ Out of 8670 *Heliphila* GBIF records, 6634 were for species with reported life history
¹⁷⁷ (Mummenhoff *et al.*, 2005), 2856 had geospatial data, 2833 did not have geospatial issues,
¹⁷⁸ 2684 were located on pixels classified as land having drought measurements, 2543 were
¹⁷⁹ located in Africa, 2192 were not duplicated. Thus, after all filtering steps, 2192 records for
¹⁸⁰ 42 species (Figure 1, Table S1) passed for further analyses. The number of samples varied
¹⁸¹ between species, with a mean of 52.19 samples per species. *H. rigidiuscula* had the most
¹⁸² records, 201, and *H. cornellsbergia* the fewest, 2 (Table S1).

¹⁸³ There were clear visual differences between the distributions of the 960 annual and the
¹⁸⁴ 1232 perennial *Heliphila* observation records (see Figure S1 for maps of individual species).
¹⁸⁵ While annual species were generally found in the western regions of South Africa and
¹⁸⁶ Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the
¹⁸⁷ occurrence of perennials extended to the east coast of South Africa (Figure 2b).

¹⁸⁸ The frequency of drought varied considerably across the ranges of *Heliphila* species
¹⁸⁹ (Figure 2c-f). This heterogeneity is expected, given that this is one of the most climatically
¹⁹⁰ diverse regions of the Earth (Sayre *et al.*, 2013). It is worth noting the east to west cline in
¹⁹¹ drought frequency observed during the summer, which distinguishes the high drought
¹⁹² frequency of the Kalahari Sands and Namid Desert phytogeographic regions from the low
¹⁹³ drought frequency of the Drakensberg Mountains and Coastal Zambesian phytogeographic
¹⁹⁴ regions. In the Cape phytogeographic region there was finer scale heterogeneity in drought
¹⁹⁵ frequency during the summer.

¹⁹⁶ Theory predicts that annuality should be adaptive in places where stresses such as
¹⁹⁷ drought are more common. Conversely, perenniability should be adaptive in places where such

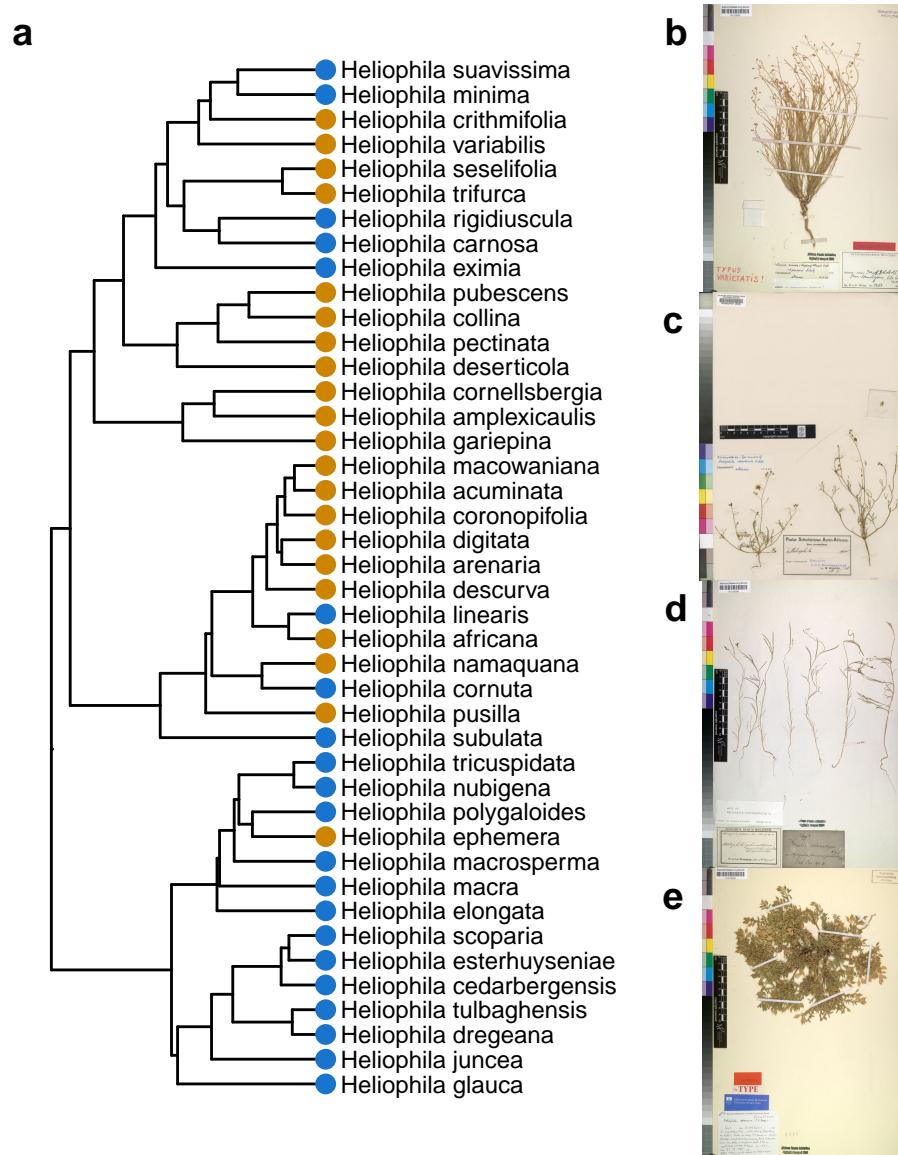


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. Example herbaria specimens accessed via GBIF of (a) *H. minima*, (b) *H. deserticola*,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

198 stresses are less frequent. We found that the frequency of drought was significantly higher at
199 the locations of occurrence records for annual species. When comparing across all occurrence

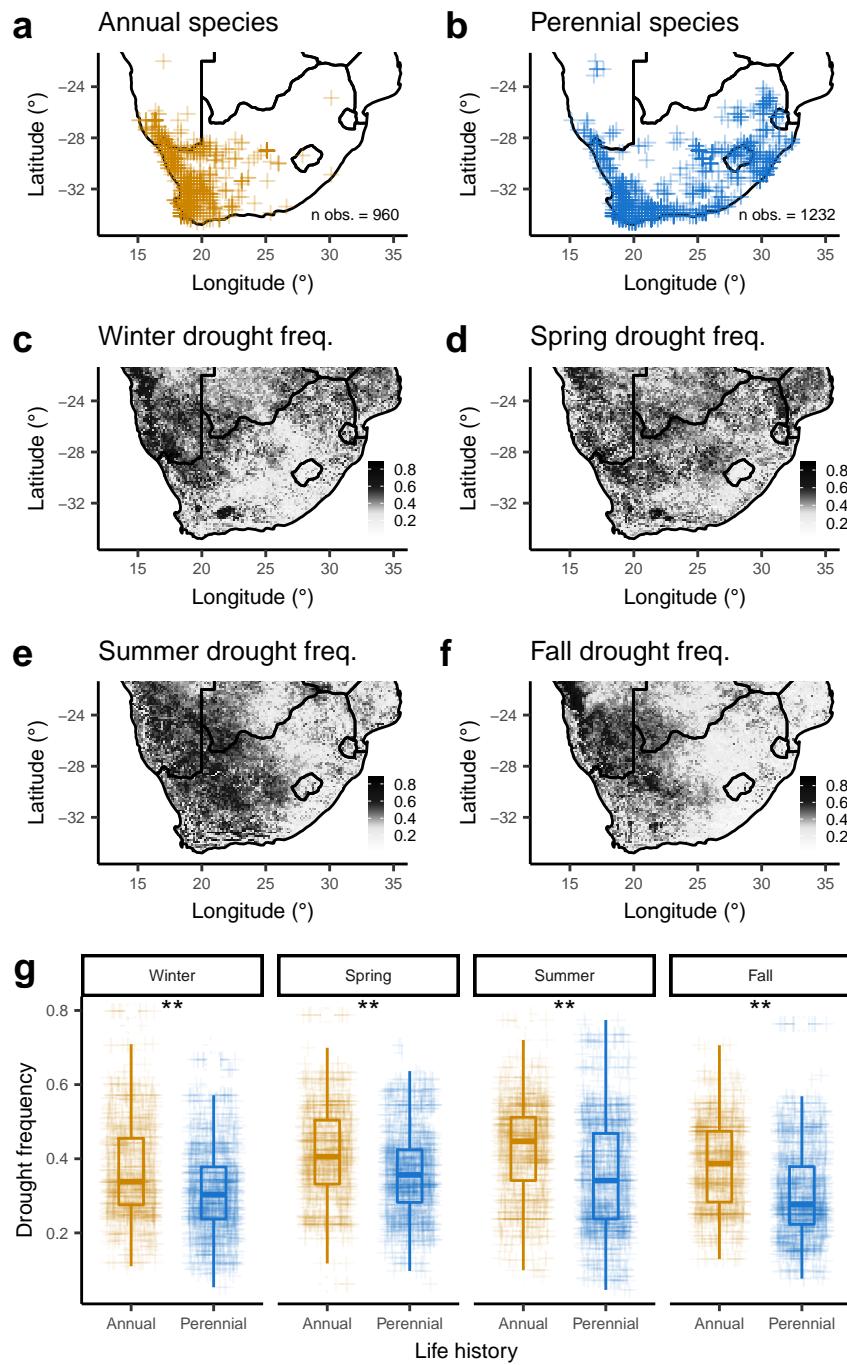


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall measured using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (t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

200 records (all records rather than species means, Figure 2g), the frequency of drought was
201 significantly higher at the location of annuals during the winter ($t = 10.65, p = 0.00$), spring
202 ($t = 10.73, p = 0.00$), summer ($t = 12.67, p = 0.00$), and fall ($t = 15.26, p = 0.00$). Because
203 a comparison across all occurrence records does not account for variation in the number of
204 records per species (Table S1) or species relatedness (Figure 1a), we also tested whether
205 mean drought frequency values of each species were significantly different between annuals
206 and perennials using phylogenetic logistic regression. We found that the mean drought
207 frequencies were significantly higher ($\alpha = 0.05$) in annual species during the spring, summer,
208 and fall (Table 1, Figure 3a). These findings indicate that common ancestry alone does not
209 explain differences the drought frequencies experienced between the environments of annual
210 and perennial *Heliophila*.

211 The preceding results indicate that annual species are found in environments where
212 droughts are significantly more frequent, especially in the summer and fall. Classic life
213 history theory hypothesizes that annuality reflects adaptation to such environments because
214 it allows species to escape stressful conditions. If this is the case, we would expect that
215 annuals spend the drought prone seasons of summer and fall as seeds. To test this
216 hypothesis, we compared the dates of occurrence records between annual and perennial
217 *Heliophila* species. The distributions reveal a considerable difference in the timing of
218 observation of these two life histories. In comparison to perennials, which appear to be
219 collected throughout the year, annuals are almost exclusively observed during the winter and
220 spring (Figure 3b). The differences between the distribution of collection dates were
221 significant by all tests ($ks.test D = 0.25, p = 0$; $bartlett.test K2 = 503.18, p = 0.00$) This is
222 consistent with a model of life history in which annual species flower in the spring, set seed,
223 senesce, and die before the summer. Thus, these annual species are likely to remain dormant
224 during the summer and fall, when drought is the strongest predictor of the distributions of
225 annual and perennial life histories (Figure 3a).

Table 1

*Phylogenetic logistic regressions between life history, and the mean drought frequency observed at specimen sites of *Heliophila* species the winter, spring, summer, and fall.*

Predictor	Estimate	P
Intercept	0.7231	0.6636
Winter drought freq.	-1.5452	0.7274
Intercept	5.0107	0.0534
Spring drought freq.	-12.9014	0.0464
Intercept	7.7093	0.0054
Summer drought freq.	-19.9056	0.0042
Intercept	7.0162	0.0082
Fall drought freq.	-20.8174	0.0067

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

226

Discussion

227 To test the hypothesis that annual and perennial plants reflect adaptation to
 228 alternative drought environments we examined the landscape distribution of life history
 229 strategies in the large and diverse mustard genus, *Heliophila*. Using metadata of 2192
 230 occurrence records and a 34 year dataset of satellite-detected droughts, we tested the
 231 prediction that annual species are more often observed in drought-prone locations than
 232 perennial species, when controlling for phylogenetic relatedness. We found that drought
 233 frequency is significantly different between the distributions of annual and perennial species,

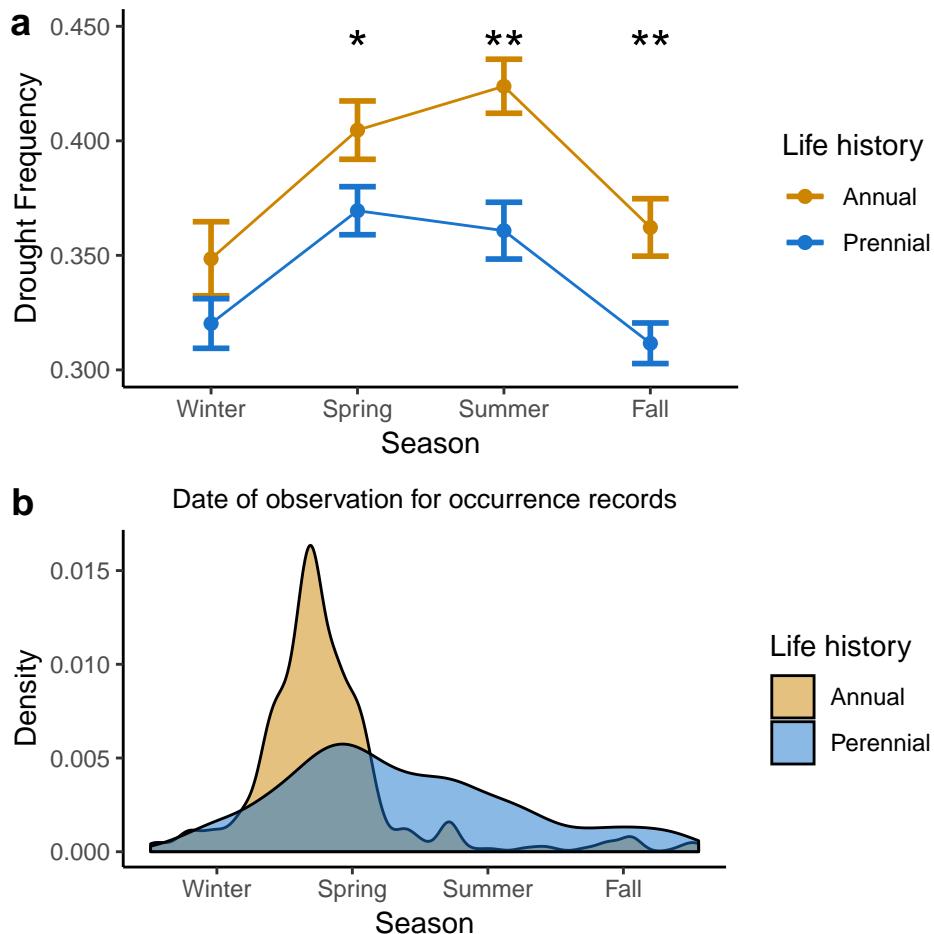


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*. (phylogenetic logistic regression, * = $p < 0.05$, ** = $p < 0.01$) (b) Collection dates of GBIF records of annual and perennial species of *Heliophila*.

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

239 We cannot eliminate the possibility that confounding traits or environmental variables

are the causative factors explaining variation in the distributions of annual and perennial species. Nevertheless, these results provide quantitative support for the classic prediction that annual species are found in environments that experience more frequent drought than perennial species. These findings complement previous reports of qualitative associations between annuality with environments characterized as having increased aridity (Evans *et al.*, 2005), alternative precipitation defined habitats (Morishima *et al.*, 1984; Datson *et al.*, 2008), 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, which represents a significant advance over relying on personal observations to characterize species distributions.

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

266 focused on describing the evolutionary origins of annuality (Barrett *et al.*, 1996; Conti *et al.*,
267 1999; Andreasen & Baldwin, 2001; Verboom *et al.*, 2004; Friedman & Rubin, 2015) there are
268 at least a few other cases where perenniability appears to have arisen from an annual ancestor
269 (Bena *et al.*, 1998; Tank & Olmstead, 2008). And while early theory predicted selection for
270 annuality when adult mortality is high (Stearns, 1992), we also find evidence that perenniability
271 could be explained by reduced frequency of drought. The phylogeny reveals several
272 transitions from annual to perennial life history (Figure 1a) and the distributions of
273 perennial *Heliophila* extend into regions where drought frequency is low (Figure 2b, Figure
274 S1). Perennials may be able to out compete annual relatives in environments where the
275 infrequency of drought favors strategies that allow plants to benefit from growth over many
276 seasons. This also suggests that annuals rely on drought as a source of disturbance for
277 seedling recruitment when competing with perennials (Corbin & D'Antonio, 2004). Indeed,
278 no annual species were observed in the low drought regions of eastern South Africa (Figure 2,
279 Figure S1).

280 These findings suggest that species with locally adaptive life history strategies could be
281 threatened by rapidly changing drought regimens (Dai, 2011). This could have impacts on
282 ecosystem functioning and processes such as carbon cycling if life history traits evolve or the
283 composition of annual and perennial species changes in response (Garnier *et al.*, 1997;
284 Roumet *et al.*, 2006; Monroe *et al.*, 2018a). Furthermore, the frequency of drought may be
285 an important factor when considering the use of perennial cropping systems (Parry *et al.*,
286 2005; Lelièvre & Volaire, 2009).

287 In conclusion, we find strong support for classic life history theory which predicts that
288 annuality is adaptive in environments where droughts occur more frequently. Additionally,
289 we report evidence consistent with a life history model in annuals in which they escape
290 drought prone seasons during the seed phase of their life cycle. Finally, we find evidence that
291 the distributions of perennial lineages may indicate a competitive advantage in areas where

292 droughts are infrequent. More broadly, this work highlights the irreplaceable value of natural
293 history collections and demonstrates the power of combining such information with large
294 scale remote sensing data to address outstanding classic hypotheses in ecology and evolution.

295

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299

Author contributions

300 JGM, BG, KGT and JKM contributed to the design of the research, interpretation,
301 and writing the manuscript. JGM, BG, and KGT contributed to the performance of the
302 research and data analysis.

303

References

- 304 AghaKouchak A, Farahmand A, Melton F, Teixeira J, Anderson M, Wardlow BD, Hain C.
305 **2015.** Remote sensing of drought: Progress, challenges and opportunities. *Reviews of*
306 *Geophysics* **53:** 452–480.
- 307 Alfaro M, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky D, Carnevale G, Harmon
308 L. **2009.** Nine exceptional radiations plus high turnover explain species diversity in
309 jawed vertebrates. *Proceedings of the National Academy of Sciences of the United*
310 *States of America* **106:** 13410–13414.
- 311 Andreasen K, Baldwin BG. **2001.** Unequal evolutionary rates between annual and perennial
312 lineages of checker mallows (sidalcea, malvaceae): Evidence from 18S–26S rDNA
313 internal and external transcribed spacers. *Molecular Biology and Evolution* **18:**
314 936–944.
- 315 Appel O, Al-Shehbaz IA. **1997.** Generic limits and taxonomy of hornungia, pritzelago, and
316 hymenolobus (brassicaceae). *Novon*: 338–340.
- 317 Aust F, Barth M. **2018.** *papaja: Create APA manuscripts with R Markdown.*
- 318 Barrett SCH, Harder LD, Worley AC. **1996.** The comparative biology of pollination and
319 mating in flowering plants. *Phil. Trans. R. Soc. Lond. B* **351:** 1271–1280.
- 320 Bates D, Maechler M. **2018.** *Matrix: Sparse and dense matrix classes and methods.*
- 321 Bena G, Lejeune B, Prosperi J-M, Olivieri I. **1998.** Molecular phylogenetic approach for
322 studying life-history evolution: The ambiguous example of the genus medicago l.
323 *Proceedings of the Royal Society of London B: Biological Sciences* **265:** 1141–1151.
- 324 Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard M, Rambaut A,
325 Drummond A. **2014.** BEAST 2: A software platform for bayesian evolutionary
326 analysis. *PLoS Computational Biology* **10:** doi:10.1371/journal.pcbi.1003537.

- 327 Brown PM. 1996. OLDLIST: A database of maximum tree ages. *Tree rings, environment,*
328 *and humanity. Radiocarbon* **1996**: 727–731.
- 329 Charnov EL, Schaffer WM. 1973. Life-history consequences of natural selection: Cole's
330 result revisited. *The American Naturalist* **107**: 791–793.
- 331 Cole LC. 1954. The population consequences of life history phenomena. *The Quarterly*
332 *Review of Biology* **29**: 103–137.
- 333 Conti E, Soltis DE, Hardig TM, Schneider J. 1999. Phylogenetic relationships of the silver
334 saxifrages (saxifraga, sect. Ligulatae haworth): Implications for the evolution of
335 substrate specificity, life histories, and biogeography. *Molecular Phylogenetics and*
336 *Evolution* **13**: 536–555.
- 337 Corbin JD, D'Antonio CM. 2004. Competition between native perennial and exotic annual
338 grasses: Implications for an historical invasion. *Ecology* **85**: 1273–1283.
- 339 Cruz-Mazo G, Buide M, Samuel R, Narbona E. 2009. Molecular phylogeny of
340 scorzoneroides (asteraceae): Evolution of heterocarpy and annual habit in
341 unpredictable environments. *Molecular phylogenetics and evolution* **53**: 835–847.
- 342 Dai A. 2011. Drought under global warming: A review. *Wiley Interdisciplinary Reviews:*
343 *Climate Change* **2**: 45–65.
- 344 Darriba D, Taboada G, Doallo R, Posada D. 2012. JModelTest 2: More models, new
345 heuristics and parallel computing. *Nature Methods* **9**: 772.
- 346 Daru BH, Park DS, Primack RB, Willis CG, Barrington DS, Whitfeld TJ, Seidler TG,
347 Sweeney PW, Foster DR, Ellison AM *et al.* 2018. Widespread sampling biases in
348 herbaria revealed from large-scale digitization. *New Phytologist* **217**: 939–955.

- 349 Datson P, Murray B, Steiner K. **2008**. Climate and the evolution of annual/perennial
350 life-histories in nemesia (scrophulariaceae). *Plant Systematics and Evolution* **270**:
351 39–57.
- 352 Davis CC, Willis CG, Connolly B, Kelly C, Ellison AM. **2015**. Herbarium records are
353 reliable sources of phenological change driven by climate and provide novel insights
354 into species' phenological cueing mechanisms. *American Journal of Botany* **102**:
355 1599–1609.
- 356 Dittberner H, Korte A, Mettler-Altmann T, Weber A, Monroe G, Meaux J de. **2018**.
357 Natural variation in stomata size contributes to the local adaptation of water-use
358 efficiency in arabidopsis thaliana. *bioRxiv*: 253021.
- 359 Eastman J, Alfaro M, Joyce P, Hipp A, Harmon L. **2011**. A novel comparative method for
360 identifying shifts in the rate of character evolution on trees. *Evolution* **65**: 3578–3589.
- 361 Evans ME, Hearn DJ, Hahn WJ, Spangle JM, Venable DL. **2005**. Climate and life-history
362 evolution in evening primroses (oenothera, onagraceae): A phylogenetic comparative
363 analysis. *Evolution* **59**: 1914–1927.
- 364 Felsenstein J. **1985**. Phylogenies and the comparative method. *American Naturalist* **125**:
365 1–15.
- 366 Franco M, Silvertown J. **1996**. Life history variation in plants: An exploration of the
367 fast-slow continuum hypothesis. *Phil. Trans. R. Soc. Lond. B* **351**: 1341–1348.
- 368 Friedman J, Rubin MJ. **2015**. All in good time: Understanding annual and perennial
369 strategies in plants. *American journal of botany* **102**: 497–499.
- 370 Garnier E, Cordonnier P, Guillerm J-L, Sonié L. **1997**. Specific leaf area and leaf nitrogen
371 concentration in annual and perennial grass species growing in mediterranean

- 372 old-fields. *Oecologia* **111**: 490–498.
- 373 GBIF. **2018**. GBIF occurrence download.
- 374 Genz A, Bretz F. **2009**. *Computation of multivariate normal and t probabilities*. Heidelberg:
375 Springer-Verlag.
- 376 Guindon S, Gascuel O. **2003**. A simple, fast and accurate method to estimate large
377 phylogenies by maximum-likelihood. *Systematic Biology* **52**: 696–704.
- 378 Hadfield JD. **2010**. MCMC methods for multi-response generalized linear mixed models:
379 The MCMCglmm R package. *Journal of Statistical Software* **33**: 1–22.
- 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*.
- 383 Henry L, Wickham H. **2018**. *Purrr: Functional programming tools*.
- 384 Hijmans RJ. **2018**. *Raster: Geographic data analysis and modeling*.
- 385 Ho LST, Ane C. **2014**. A linear-time algorithm for gaussian and non-gaussian trait
386 evolution models. *Systematic Biology* **63**: 397–408.
- 387 Ives A, Garland T. **2010**. CPhylogenetic logistic regression for binary dependent variables.
388 *Systematic Biology* **59**: 9–26.
- 389 Katoh, Misawa, Kuma, Miyata. **2002**. MAFFT: A novel method for rapid multiple
390 sequence alignment based on fast fourier transform. *Nucleic Acids Research* **30**:
391 3059–3066.

- 392 Kerr JT, Ostrovsky M. **2003**. From space to species: Ecological applications for remote
393 sensing. *Trends in ecology & evolution* **18**: 299–305.
- 394 Kogan FN. **2001**. Operational space technology for global vegetation assessment. *Bulletin
395 of the American Meteorological Society* **82**: 1949–1964.
- 396 Kogan F, Guo W, Strashnaia A, Kleshenko A, Chub O, Virchenko O. **2016**. Modelling and
397 prediction of crop losses from noaa polar-orbiting operational satellites. *Geomatics,
398 Natural Hazards and Risk* **7**: 886–900.
- 399 Lang PL, Willems FM, Scheepens J, Burbano HA, Bossdorf O. **2018**. *Using herbaria to
400 study global environmental change*. PeerJ Preprints.
- 401 Lelièvre F, Volaire F. **2009**. Current and potential development of perennial grasses in
402 rainfed mediterranean farming systems. *Crop Science* **49**: 2371–2378.
- 403 Mandáková T, Mummenhoff K, Al-Shehbaz IA, Mucina L, Mühlhausen A, Lysak MA.
404 **2012**. Whole-genome triplication and species radiation in the southern african tribe
405 heliophileae (brassicaceae). *Taxon* **61**: 989–1000.
- 406 Miller M, Pfeiffer W, Schwartz T and. **2010**. Creating the cipres science gateway for
407 inference of large phylogenetic trees. *Proceedings of the Gateway Computing
408 Environments Workshop*: 1–8.
- 409 Mojica JP, Mullen J, Lovell JT, Monroe JG, Paul JR, Oakley CG, McKay JK. **2016**.
410 Genetics of water use physiology in locally adapted *Arabidopsis thaliana*. *Plant
411 Science*.
- 412 Monroe J, Markman D, Beck W, Felton A, Vahsen M, Pressler Y. **2018a**. Ecoevolutionary
413 dynamics of carbon cycling in the anthropocene. *Trends in ecology & evolution* **33**:
414 213–225.

- 415 Monroe J, Powell T, Price N, Mullen J, Howard A, Evans K, Lovell J, McKay J. **2018b**.
416 Drought adaptation in nature by extensive genetic loss-of-function. *eLife*: DOI:
417 10.7554/eLife.41038.
- 418 Morishima H, Sano Y, Oka H. **1984**. Differentiation of perennial and annual types due to
419 habitat conditions in the wild rice *Oryza perennis*. *Plant Systematics and Evolution*
420 **144**: 119–135.
- 421 Mummenhoff K, Al-Shehbaz IA, Bakker FT, Linder HP, Mühlhausen A. **2005**. Phylogeny,
422 morphological evolution, and speciation of endemic brassicaceae genera in the cape
423 flora of southern africa. *Annals of the Missouri Botanical Garden*: 400–424.
- 424 Müller K. **2018**. *Bindrcpp: An 'rcpp' interface to active bindings*.
- 425 Müller K, Wickham H. **2018**. *Tibble: Simple data frames*.
- 426 Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. **2018**. *Caper:*
427 *Comparative analyses of phylogenetics and evolution in r*.
- 428 Paradis E, Schliep K. **2018**. Ape 5.0: An environment for modern phylogenetics and
429 evolutionary analyses in R. *Bioinformatics* **xx**: xxx–xxx.
- 430 Parry M, Flexas J, Medrano H. **2005**. Prospects for crop production under drought:
431 Research priorities and future directions. *Annals of Applied Biology* **147**: 211–226.
- 432 Pebesma EJ, Bivand RS. **2005**. Classes and methods for spatial data in R. *R News* **5**: 9–13.
- 433 Plummer M, Best N, Cowles K, Vines K. **2006**. CODA: Convergence diagnosis and output
434 analysis for mcmc. *R News* **6**: 7–11.
- 435 R by Thomas Lumley VJCP to, author. BRN that maintainers are not available to give
436 advice on using a package they did not. **2015**. *Gee: Generalized estimation equation*

solver.

- 438 R Core Team. **2018**. *R: A language and environment for statistical computing*. Vienna,
439 Austria: R Foundation for Statistical Computing.

440 Revell LJ. **2012**. Phytools: An r package for phylogenetic comparative biology (and other
441 things). *Methods in Ecology and Evolution* **3**: 217–223.

442 Richard A. Becker OS code by, Ray Brownrigg. Enhancements by Thomas P Minka ARWR
443 version by, Deckmyn. A. **2018**. *Maps: Draw geographical maps*.

444 Rojas O, Vrieling A, Rembold F. **2011**. Assessing drought probability for agricultural areas
445 in africa with coarse resolution remote sensing imagery. *Remote sensing of
446 Environment* **115**: 343–352.

447 Roumet C, Urcelay C, Di'az S. **2006**. Suites of root traits differ between annual and
448 perennial species growing in the field. *New phytologist* **170**: 357–368.

449 Sayre RG, Comer P, Hak J, Josse C, Bow J, Warner H, Larwanou M, Kelbessa E, Bekele
450 T, Kehl H *et al.* **2013**. A new map of standardized terrestrial ecosystems of africa.
451 *African Geographical Review*.

452 Schaffer W, Gadgil M. **1975**. Selection for optimal life histories in plants. *Ecology and
453 evolution of communities*.: 142–157.

454 Slater G, Harmon L, Wegmann D, Joyce P, Revell L, Alfaro M. **2012**. Fitting models of
455 continuous trait evolution to incompletely sampled comparative data using
456 approximate bayesian computation. *Evolution* **66**: 752–762.

457 Soetaert K. **2017**. *Diagram: Functions for visualising simple graphs (networks), plotting
458 flow diagrams*.

- 459 Soetaert K. **2018**. *Shape: Functions for plotting graphical shapes, colors.*
- 460 Soltis PS. **2017**. Digitization of herbaria enables novel research. *American journal of botany*
461 **104**: 1281–1284.
- 462 Stearns SC. **1992**. *The evolution of life histories.*
- 463 Stropp J, Ladle RJ, M. Malhado AC, Hortal J, Gaffuri J, H. Temperley W, Olav Skøien J,
464 Mayaux P. **2016**. Mapping ignorance: 300 years of collecting flowering plants in
465 africa. *Global Ecology and Biogeography* **25**: 1085–1096.
- 466 Tank DC, Olmstead RG. **2008**. From annuals to perennials: Phylogeny of subtribe
467 castillejinae (orobanchaceae). *American Journal of Botany* **95**: 608–625.
- 468 Thiers B. **2016**. Index herbariorum: A global directory of public herbaria and associated
469 staff. New york botanical garden’s virtual herbarium. <http://sweetgum.nybg.org/ih>.
- 470 Václavík T, Beckmann M, Cord AF, Bindewald AM. **2017**. Effects of uv-b radiation on
471 leaf hair traits of invasive plants—combining historical herbarium records with novel
472 remote sensing data. *PloS one* **12**: e0175671.
- 473 Venables WN, Ripley BD. **2002**. *Modern applied statistics with s*. New York: Springer.
- 474 Verboom GA, Linder HP, Stock WD. **2004**. Testing the adaptive nature of radiation:
475 Growth form and life history divergence in the african grass genus ehrharta (poaceae:
476 Ehrhartoideae). *American Journal of Botany* **91**: 1364–1370.
- 477 Wickham H. **2016**. *Ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.
- 478 Wickham H. **2017**. *Tidyverse: Easily install and load the ‘tidyverse’*.
- 479 Wickham H. **2018a**. *Forcats: Tools for working with categorical variables (factors)*.

- 480 Wickham H. **2018b.** *Stringr: Simple, consistent wrappers for common string operations.*
- 481 Wickham H, François R, Henry L, Müller K. **2018.** *Dplyr: A grammar of data*
482 *manipulation.*
- 483 Wickham H, Henry L. **2018.** *Tidyr: Easily tidy data with 'spread()' and 'gather()'* functions.
- 484 Wickham H, Hester J, Francois R. **2017.** *Readr: Read rectangular text data.*
- 485 Willis CG, Ellwood ER, Primack RB, Davis CC, Pearson KD, Gallinat AS, Yost JM,
486 Nelson G, Mazer SJ, Rossington NL *et al.* **2017.** Old plants, new tricks:
487 Phenological research using herbarium specimens. *Trends in ecology & evolution* **32:**
488 531–546.
- 489 Wolf A, Zimmerman NB, Anderegg WR, Busby PE, Christensen J. **2016.** Altitudinal shifts
490 of the native and introduced flora of California in the context of 20th-century
491 warming. *Global ecology and biogeography* **25:** 418–429.

492

Supplement

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

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

513

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.