

¹ Drought regimens predict life history strategies in *Heliophila*

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11

Abstract

12

Summary

13 Explaining variation in life history strategies is an enduring goal of evolutionary biology
14 and ecology. Early theory predicted that for plants, annual and perennial life histories reflect
15 adaptation to environments that experience alternative drought regimens. Nevertheless,
16 empirical support for this hypothesis from comparative analyses remains lacking.

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

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

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

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

32 Drought regimens predict life history strategies in *Heliophila*

33 **Introduction**

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

49 Classical theory predicts shorter life spans in environments where adult mortality is
50 high (Charnov & Schaffer, 1973; Stearns, 1992; Franco & Silvertown, 1996). Because lack of
51 water is perhaps the greatest threat to survival during vegetative or reproductive growth in
52 plants, this theory has been extended to the hypothesis that annuality is adaptive when it
53 allows plants to escape drought (Schaffer & Gadgil, 1975). Indeed, adaptation to drought,
54 defined as episodes of increased aridity causing plant stress (Passioura, 1996), is often invoked
55 as an explanation for the success of annual species. And while a few cases are cited where
56 annuality appears to be more common in environments with greater aridity (Stebbins Jr,

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

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

78 In addition to drought escape in annuals as a mechanism of adaptation to frequent and
79 predictable droughts, droughts may be necessary for the success of annuals more generally by
80 acting as episodes of disturbance that provide opportunities for annuals to establish and
81 compete with sympatric perennial species. Indeed, there is evidence that perennials dominate
82 in environments where disturbance events are infrequent (Rees & Long, 1992; Corbin &

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

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

104

Materials and Methods

105 **Data**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

127 Willis *et al.*, 2017; Lang *et al.*, 2018). And as they become digitized (Soltis, 2017), herbaria

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

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

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

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

¹³² *al.* (2012). Individual ITS I and II sequences for *Aethionema grandiflorum*, *Alliaria petiolata*,
¹³³ *Cardamine matthioli*, *Chamira circaeoides*, and *Rorippa amphibia* were downloaded from
¹³⁴ Genbank.

¹³⁵ **Satellite-detected drought data.** Remotely sensed data is a powerful tool for
¹³⁶ characterizing seasonal patterns in drought because it is less limited in spatial and temporal
¹³⁷ scope and resolution than weather stations or field observations (AghaKouchak *et al.*, 2015).
¹³⁸ From an ecological perspective, droughts are best defined as episodes of plant stress caused
¹³⁹ by elevated aridity (Passioura, 1996). Thus remote sensing offers the additional benefit for
¹⁴⁰ studying drought as an agent of natural selection because plant stress caused by drought can
¹⁴¹ be observed from space (Kogan, 1995a). The remotely sensed Vegetative Health Index (VHI)
¹⁴² is one such metric, which detects landscape scale reductions in plant cover and temperature
¹⁴³ conditions characteristic of drought (Kogan, 2001). Generated from data collected by NOAA
¹⁴⁴ AVHRR satellites since 1981, the VHI is a composite index combining Normalized Difference
¹⁴⁵ Vegetation Index (NDVI) derived quantification of vegetative stress (Vegetative Condition
¹⁴⁶ Index - VCI) with temperature stress indicated by anomalies in thermal spectra
¹⁴⁷ (Temperature Condition Index - TCI). These indices were developed to create an unbiased
¹⁴⁸ quantification of drought across ecosystem types. The VHI of year y during week w of [1, 52]
¹⁴⁹ at pixel i is derived from the following equations, where n is the number of years observed.

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

¹⁵⁰ Low values of VCI indicate episodes when plant cover is particularly low for a given
¹⁵¹ location during a given time of the year. Thus, it controls for the location and season in
¹⁵² quantifying plant stress.

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

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

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

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

169 Analyses

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

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

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

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

189 **Phylogeny construction and ancestral state estimation.** Outgroup (

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

199 Ancestral state estimation was performed in R using the package phytools (Revell, 2012) to
200 generate 10,000 stochastic character maps simulated under an equal rates model of character
201 evolution for the trait life habit (annual or perennial).

202 Comparison of drought frequency between annual and perennial species.

203 To evaluate the hypothesis that annual and perennial life history strategies reflect
204 adaptations to alternative drought regimens, we tested the corresponding prediction that the
205 observed distributions of annual and perennial *Heliophila* species would be significantly
206 associated with historic drought frequency. First, we compared the frequency of drought
207 across all occurrence records of between annual and perennial species by t-tests. Independent
208 tests were performed to compare drought frequency between annuals and perennials during
209 each season. We also tested for a relationship between drought frequency and life history,
210 season, and their interaction by analysis of variance while including species as a random
211 effect. To account for variation in the number of occurrence records per species, we next
212 calculated the mean drought frequency during the winter, spring, summer and fall for each
213 species. Because shared evolutionary history of closely related species can lead to spurious
214 associations between traits and environments (Felsenstein, 1985), we tested for a relationship
215 between life history strategy and drought frequency while controlling for phylogeny using
216 phylogenetic logistic regression (Ives & Garland, 2010). This statistical approach is designed
217 to control for the confounding effects of common ancestry's influence on demographic
218 features such as geospatial relationships when addressing hypotheses about the role of
219 natural selection on trait distributions.

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

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

224 Results

225 The topology of the estimated *Heliophila* phylogeny was consistent with previous

226 studies (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). Based on 10,000 stochastic

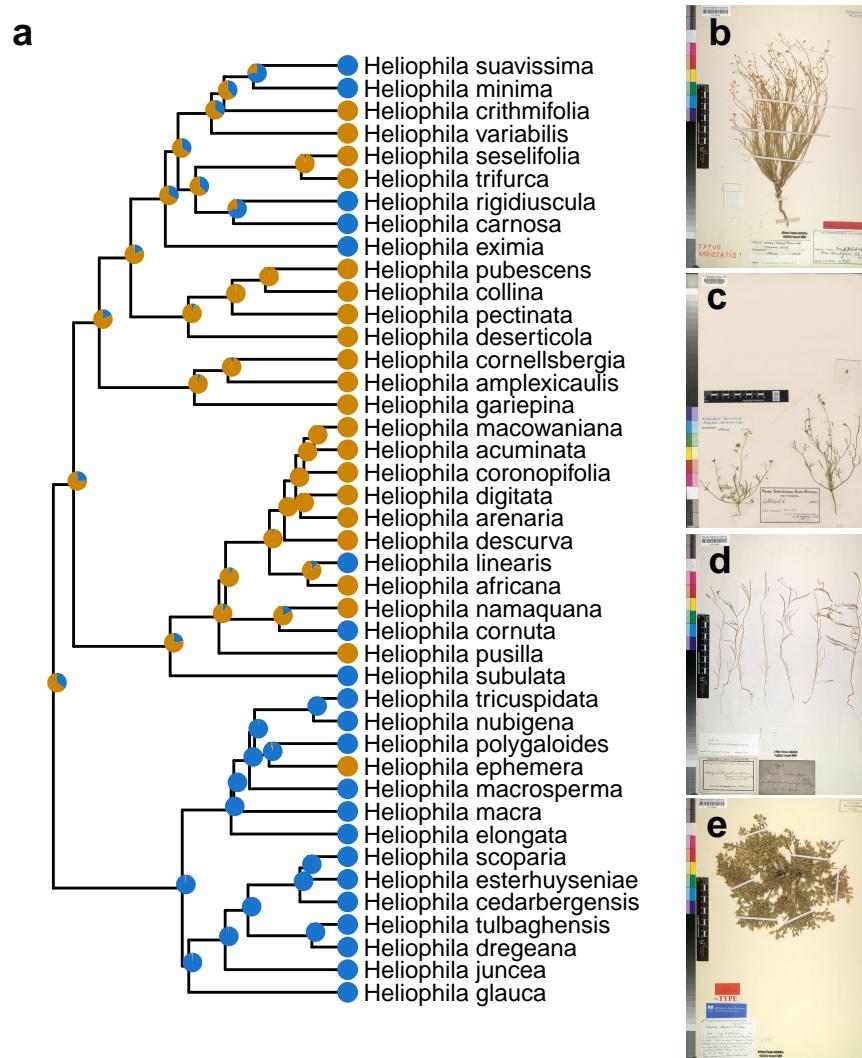


Figure 1. Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. At internal nodes, pie charts indicate the estimated posterior probability of being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

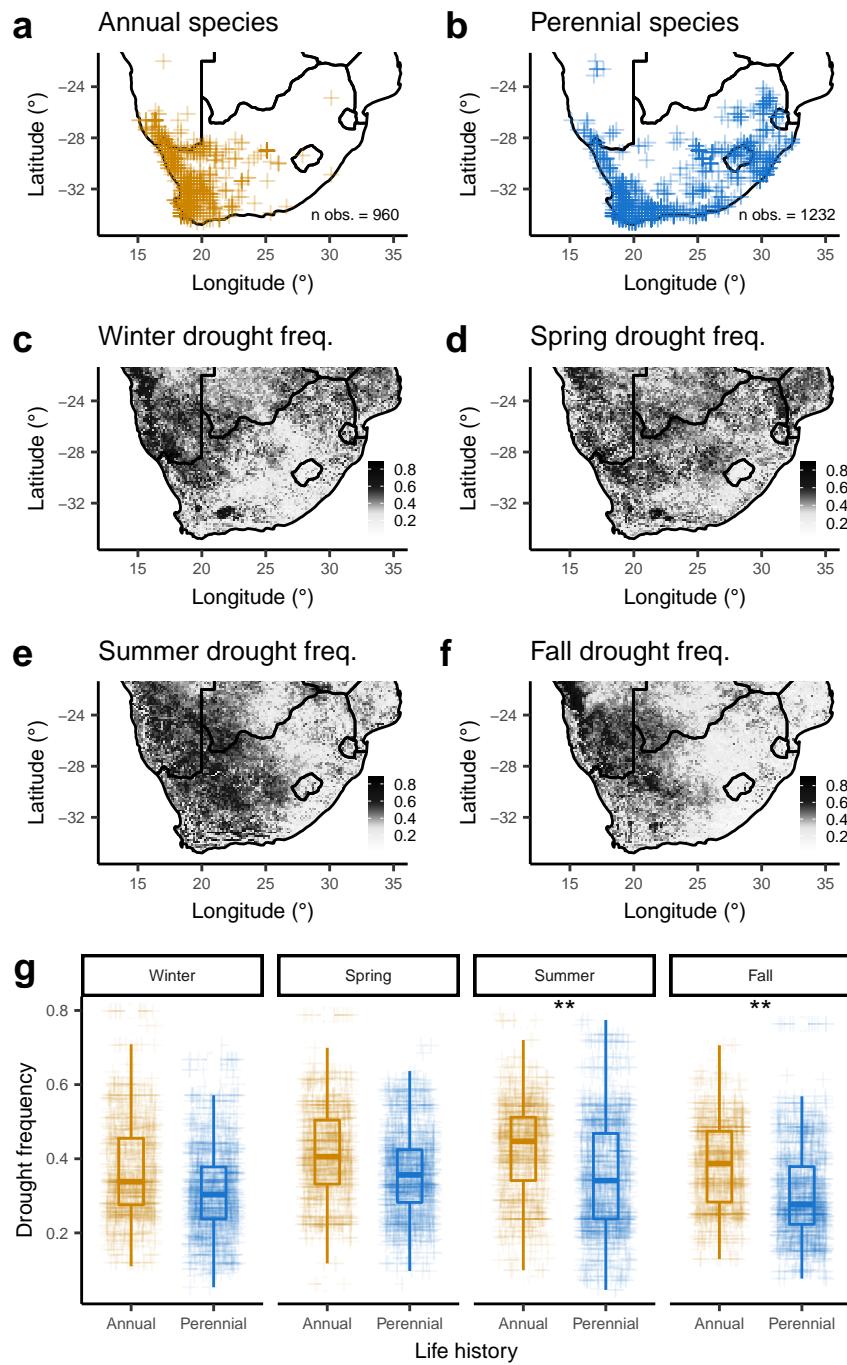


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall detected using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (Post-hoc contrasts annuals and perennials from ANOVA, ** = p < 0.01).

character maps simulated under an equal rates model of character evolution in life history, an average of approximately eight changes from annual to perennial and five changes from perennial to annual are observed per stochastic character map (Figure 1a). These results suggest that the ancestral state of *Heliophila* was annual and that both character states have arisen independently multiple times.

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

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

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

We found that the frequency of drought was significantly higher at the locations of occurrence records for annual species. When comparing across all occurrence records (all records rather than species means, Figure 2g), a mixed-model analysis of variance which included species as random effect revealed a significant relationship between drought frequency and life history ($p < 0.01$), season ($p < 0.01$) and their interaction ($p < 0.01$) (Table S2). Post-hoc contrasts showed that the frequency of drought was significantly higher at the location of annuals during the summer (z ratio = 3.93, $p = < 0.01$), and fall (z ratio = 4.06, $p < 0.01$). Because a comparison across all occurrence records does not account for variation in the number of records per species (Table S1) or species relatedness (Figure 1a), we also tested whether mean drought frequency values of each species were significantly different between annuals and perennials using phylogenetic logistic regression. We found that the mean drought frequencies were significantly higher ($\alpha = 0.05$) in annual species during the spring, summer, and fall (Table 1, Figure 3a,b). These findings indicate that common ancestry alone does not explain differences in the drought frequencies experienced between the environments of annual and perennial *Heliophila*.

The preceding results indicate that annual species are found in environments where droughts are significantly more frequent, especially in the summer and fall. Classic life history theory hypothesizes that annuality reflects adaptation to such environments because it allows species to escape predictable stressful conditions. If this is the case, we would expect that annuals spend the drought prone seasons of summer and fall as seeds. To test this hypothesis, we compared the dates of occurrence records between annual and perennial *Heliophila* species. The distributions reveal a considerable difference in the timing of observation of these two life histories. In comparison to perennials, which appear to be collected throughout the year, annuals are almost exclusively observed during the winter and spring (Figure 3b). The differences between the distribution of collection dates were significant by all tests ($ks.test D = 0.25, p < 0.01$; $bartlett.test K2 = 503.18, p < 0.01$) This is consistent with a model of life history in which annual species flower in the spring, set

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.

²⁸⁰ seed, senesce, and die before the summer. Thus, these annual species are likely to remain
²⁸¹ dormant during the summer and fall, when drought is the strongest predictor of the
²⁸² distributions of annual and perennial life histories (Figure 3a).

²⁸³

Discussion

²⁸⁴ To test the hypothesis that annual and perennial plants reflect adaptation to
²⁸⁵ alternative drought environments we examined the landscape distribution of life history
²⁸⁶ strategies in the large and diverse mustard genus, *Heliophila*. Using metadata of 2192

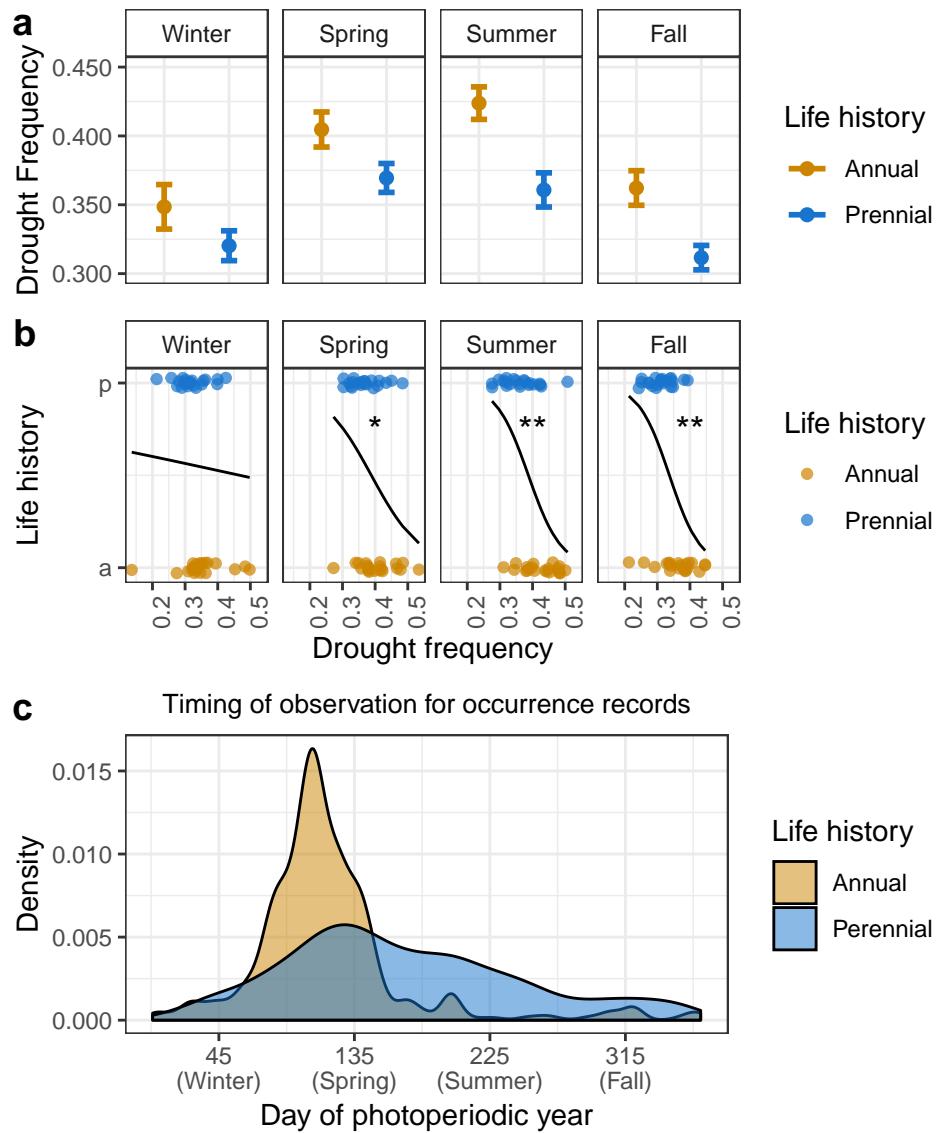


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons calculated at the occurrence locations of GBIF records of annual and perennial species of *Heliophila*. (b) Results from phylogenetic logistic regression, where the line shows the model fit and * = $p < 0.05$, ** = $p < 0.01$. Annuals were scored as 0 and perennials as 1. (c) Collection dates of GBIF records of annual and perennial species of *Heliophila* in relation to the photoperiodic calendar where day 1 is intermediate to the fall equinox and winter solstice.

287 occurrence records and a 34 year dataset of satellite-detected droughts, we tested the
 288 prediction that annual species are more often observed in drought-prone locations than

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

296 We cannot eliminate the possibility that confounding traits or environmental variables
297 are the causative factors explaining variation in the distributions of annual and perennial
298 species. Nevertheless, these results provide quantitative support for the classic prediction
299 that annual species are found in environments that experience more frequent drought than
300 perennial species, building on previous investigations of associations between life history and
301 climate (Morishima *et al.*, 1984; Evans *et al.*, 2005; Datson *et al.*, 2008; Cruz-Mazo *et al.*,
302 2009). To our knowledge this is the first study to demonstrate a significant association
303 between life history and drought in a phylogenetic context informed by large scale species
304 distribution data and long term drought detection.

305 Unfortunately, herbarium collections and their associated data do not represent
306 systematic or random sampling of a species distribution. Significant biases in collecting exist,
307 which we have not necessarily controlled for here, and may have some effect on our findings,
308 such as a bias toward collecting near roads or near the locations of natural history collections
309 (Daru *et al.*, 2018). Future research will benefit from systematic sampling efforts to avoid
310 these noted biases. However, the ecosystems of southern Africa include several biodiversity
311 hotspots and are among the most botanically well sampled regions on Earth (Daru *et al.*,
312 2018), suggesting that this may currently be the optimal region for our analyses of life
313 history distribution. Indeed, we were able to use 2192 occurrence records to study 42 species,
314 which represents a significant advance over relying on personal observations to characterize

315 species distributions.

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

336 These findings suggest that species with locally adaptive life history strategies could be
337 threatened by rapidly changing drought regimens (Dai, 2011). In light of the findings here,
338 forecasted reductions in rainfall across eastern South Africa (Service & Comission, 2017)
339 could be particularly impactful to plant community compositions. Here we found that this
340 region is currently dominated by derived perennial species of *Heliophila*. However, a scenario

341 in which droughts become more frequent in this region may allow for the establishment of
342 annuals. Such changes in selection patterns and shifts in plant functional diversity could
343 have impacts on ecosystem functioning and processes such as carbon cycling (Garnier *et al.*,
344 1997; Roumet *et al.*, 2006; Monroe *et al.*, 2018a). Furthermore, the changes in frequency of
345 drought may be an important factor when considering the use of perennial cropping systems
346 (Parry *et al.*, 2005; Lelièvre & Volaire, 2009).

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

355 **Acknowledgments**

356 We thank Jesse Lasky, members of the Sloan lab, and three anonymous reviewers for
357 generous feedback that improved the quality of this work. This research was supported by
358 NSF Award 1701918 and USDA-NIFA Award 2014-38420-21801 to JGM.

359 **Author contributions**

360 JGM, BG, KGT and JKM contributed to the design of the research, interpretation,
361 and writing the manuscript. JGM, BG, and KGT contributed to the performance of the
362 research and data analysis.

363

References

- 364 AghaKouchak A, Farahmand A, Melton F, Teixeira J, Anderson M, Wardlow BD, Hain C.
365 **2015.** Remote sensing of drought: Progress, challenges and opportunities. *Reviews of*
366 *Geophysics* **53:** 452–480.
- 367 Andreasen K, Baldwin BG. **2001.** Unequal evolutionary rates between annual and perennial
368 lineages of checker mallows (*sidalcea*, malvaceae): Evidence from 18S–26S rDNA
369 internal and external transcribed spacers. *Molecular Biology and Evolution* **18:**
370 936–944.
- 371 Appel O, Al-Shehbaz IA. **1997.** Generic limits and taxonomy of hornungia, pritzelago, and
372 hymenolobus (brassicaceae). *Novon*: 338–340.
- 373 Barrett SCH, Harder LD, Worley AC. **1996.** The comparative biology of pollination and
374 mating in flowering plants. *Phil. Trans. R. Soc. Lond. B* **351:** 1271–1280.
- 375 Bena G, Lejeune B, Prosperi J-M, Olivier I. **1998.** Molecular phylogenetic approach for
376 studying life-history evolution: The ambiguous example of the genus medicago l.
377 *Proceedings of the Royal Society of London B: Biological Sciences* **265:** 1141–1151.
- 378 Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard M, Rambaut A,
379 Drummond A. **2014.** BEAST 2: A software platform for bayesian evolutionary
380 analysis. *PLoS Computational Biology* **10:** doi:10.1371/journal.pcbi.1003537.
- 381 Brown PM. **1996.** OLDLIST: A database of maximum tree ages. *Tree rings, environment,*
382 *and humanity. Radiocarbon* **1996:** 727–731.
- 383 Charnov EL, Schaffer WM. **1973.** Life-history consequences of natural selection: Cole's
384 result revisited. *The American Naturalist* **107:** 791–793.

- 385 Clary J. **2012**. Determinants of perennial and annual grass distribution in
386 mediterranean-climate California. *Plant Ecology* **213**: 1203–1208.
- 387 Cole LC. **1954**. The population consequences of life history phenomena. *The Quarterly
388 Review of Biology* **29**: 103–137.
- 389 Conti E, Soltis DE, Hardig TM, Schneider J. **1999**. Phylogenetic relationships of the silver
390 saxifrages (saxifraga, sect. Ligulatae Haworth): Implications for the evolution of
391 substrate specificity, life histories, and biogeography. *Molecular Phylogenetics and
392 Evolution* **13**: 536–555.
- 393 Corbin JD, D'Antonio CM. **2004**. Competition between native perennial and exotic annual
394 grasses: Implications for an historical invasion. *Ecology* **85**: 1273–1283.
- 395 Cruz-Mazo G, Buide M, Samuel R, Narbona E. **2009**. Molecular phylogeny of
396 scorzoneroideae (Asteraceae): Evolution of heterocarpy and annual habit in
397 unpredictable environments. *Molecular phylogenetics and evolution* **53**: 835–847.
- 398 Dai A. **2011**. Drought under global warming: A review. *Wiley Interdisciplinary Reviews:
399 Climate Change* **2**: 45–65.
- 400 Darriba D, Taboada G, Doallo R, Posada D. **2012**. JModelTest 2: More models, new
401 heuristics and parallel computing. *Nature Methods* **9**: 772.
- 402 Daru BH, Park DS, Primack RB, Willis CG, Barrington DS, Whitfeld TJ, Seidler TG,
403 Sweeney PW, Foster DR, Ellison AM *et al.* **2018**. Widespread sampling biases in
404 herbaria revealed from large-scale digitization. *New Phytologist* **217**: 939–955.
- 405 Datson P, Murray B, Steiner K. **2008**. Climate and the evolution of annual/perennial
406 life-histories in nemesia (Scrophulariaceae). *Plant Systematics and Evolution* **270**:
407 39–57.

- 408 Davis CC, Willis CG, Connolly B, Kelly C, Ellison AM. **2015**. Herbarium records are
409 reliable sources of phenological change driven by climate and provide novel insights
410 into species' phenological cueing mechanisms. *American Journal of Botany* **102**:
411 1599–1609.
- 412 Dittberner H, Korte A, Mettler-Altmann T, Weber A, Monroe G, Meaux J de. **2018**.
413 Natural variation in stomata size contributes to the local adaptation of water-use
414 efficiency in *arabidopsis thaliana*. *bioRxiv*: 253021.
- 415 Evans ME, Hearn DJ, Hahn WJ, Spangle JM, Venable DL. **2005**. Climate and life-history
416 evolution in evening primroses (*oenothera*, *onagraceae*): A phylogenetic comparative
417 analysis. *Evolution* **59**: 1914–1927.
- 418 Felsenstein J. **1985**. Phylogenies and the comparative method. *American Naturalist* **125**:
419 1–15.
- 420 Franco M, Silvertown J. **1996**. Life history variation in plants: An exploration of the
421 fast-slow continuum hypothesis. *Phil. Trans. R. Soc. Lond. B* **351**: 1341–1348.
- 422 Friedman J, Rubin MJ. **2015**. All in good time: Understanding annual and perennial
423 strategies in plants. *American journal of botany* **102**: 497–499.
- 424 Garnier E, Cordonnier P, Guillerm J-L, Sonié L. **1997**. Specific leaf area and leaf nitrogen
425 concentration in annual and perennial grass species growing in mediterranean
426 old-fields. *Oecologia* **111**: 490–498.
- 427 GBIF. **2018**. GBIF occurrence download.
- 428 Guindon S, Gascuel O. **2003**. A simple, fast and accurate method to estimate large
429 phylogenies by maximum-likelihood. *Systematic Biology* **52**: 696–704.
- 430 Ives A, Garland T. **2010**. CPhylogenetic logistic regression for binary dependent variables.

- 431 *Systematic Biology* **59**: 9–26.
- 432 Katoh, Misawa, Kuma, Miyata. **2002**. MAFFT: A novel method for rapid multiple
433 sequence alignment based on fast fourier transform. *Nucleic Acids Research* **30**:
434 3059–3066.
- 435 Kerr JT, Ostrovsky M. **2003**. From space to species: Ecological applications for remote
436 sensing. *Trends in ecology & evolution* **18**: 299–305.
- 437 Kogan FN. **1995a**. Droughts of the late 1980s in the united states as derived from noaa
438 polar-orbiting satellite data. *Bulletin of the American Meteorological Society* **76**:
439 655–668.
- 440 Kogan FN. **1995b**. Application of vegetation index and brightness temperature for drought
441 detection. *Advances in space research* **15**: 91–100.
- 442 Kogan FN. **2001**. Operational space technology for global vegetation assessment. *Bulletin
443 of the American Meteorological Society* **82**: 1949–1964.
- 444 Kogan F, Guo W, Strashnaia A, Kleshenko A, Chub O, Virchenko O. **2016**. Modelling and
445 prediction of crop losses from noaa polar-orbiting operational satellites. *Geomatics,
446 Natural Hazards and Risk* **7**: 886–900.
- 447 Lang PL, Willems FM, Scheepens J, Burbano HA, Bossdorf O. **2018**. *Using herbaria to
448 study global environmental change*. PeerJ Preprints.
- 449 Lelièvre F, Volaire F. **2009**. Current and potential development of perennial grasses in
450 rainfed mediterranean farming systems. *Crop Science* **49**: 2371–2378.
- 451 Mandáková T, Mummenhoff K, Al-Shehbaz IA, Mucina L, Mühlhausen A, Lysak MA.
452 **2012**. Whole-genome triplication and species radiation in the southern african tribe
453 heliophileae (brassicaceae). *Taxon* **61**: 989–1000.

- 454 Miller M, Pfeiffer W, Schwartz T and. **2010**. Creating the cipres science gateway for
455 inference of large phylogenetic trees. *Proceedings of the Gateway Computing*
456 *Environments Workshop*: 1–8.
- 457 Mojica JP, Mullen J, Lovell JT, Monroe JG, Paul JR, Oakley CG, McKay JK. **2016**.
458 Genetics of water use physiology in locally adapted *Arabidopsis thaliana*. *Plant*
459 *Science*.
- 460 Monroe J, Markman D, Beck W, Felton A, Vahsen M, Pressler Y. **2018a**. Ecoevolutionary
461 dynamics of carbon cycling in the anthropocene. *Trends in ecology & evolution* **33**:
462 213–225.
- 463 Monroe J, Powell T, Price N, Mullen J, Howard A, Evans K, Lovell J, McKay J. **2018b**.
464 Drought adaptation in nature by extensive genetic loss-of-function. *eLife*: DOI:
465 10.7554/eLife.41038.
- 466 Monyela BM. **2017**. A two-year long drought in summer 2014/2015 and 2015/2016 over
467 south africa.
- 468 Morishima H, Sano Y, Oka H. **1984**. Differentiation of perennial and annual types due to
469 habitat conditions in the wild rice *Oryza perennis*. *Plant Systematics and Evolution*
470 **144**: 119–135.
- 471 Mummenhoff K, Al-Shehbaz IA, Bakker FT, Linder HP, Mühlhausen A. **2005**. Phylogeny,
472 morphological evolution, and speciation of endemic brassicaceae genera in the cape
473 flora of southern africa. *Annals of the Missouri Botanical Garden*: 400–424.
- 474 Parry M, Flexas J, Medrano H. **2005**. Prospects for crop production under drought:
475 Research priorities and future directions. *Annals of Applied Biology* **147**: 211–226.
- 476 Passioura J. **1996**. Drought and drought tolerance. *Plant growth regulation* **20**: 79–83.

- 477 Rees M, Long MJ. **1992**. Germination biology and the ecology of annual plants. *The
478 American Naturalist* **139**: 484–508.
- 479 Revell LJ. **2012**. Phytools: An r package for phylogenetic comparative biology (and other
480 things). *Methods in Ecology and Evolution* **3**: 217–223.
- 481 Rojas O, Vrieling A, Rembold F. **2011**. Assessing drought probability for agricultural areas
482 in africa with coarse resolution remote sensing imagery. *Remote sensing of
483 Environment* **115**: 343–352.
- 484 Roumet C, Urcelay C, Di'az S. **2006**. Suites of root traits differ between annual and
485 perennial species growing in the field. *New phytologist* **170**: 357–368.
- 486 Sayre RG, Comer P, Hak J, Josse C, Bow J, Warner H, Larwanou M, Kelbessa E, Bekele
487 T, Kehl H *et al.* **2013**. A new map of standardized terrestrial ecosystems of africa.
488 *African Geographical Review*.
- 489 Schaffer W, Gadgil M. **1975**. Selection for optimal life histories in plants. *Ecology and
490 evolution of communities.*: 142–157.
- 491 Service SAW, Comission WR. **2017**. *A climate change reference atlas*.
- 492 Soltis PS. **2017**. Digitization of herbaria enables novel research. *American journal of botany
493* **104**: 1281–1284.
- 494 Stearns SC. **1992**. *The evolution of life histories*.
- 495 Stebbins Jr GL. **1952**. Aridity as a stimulus to plant evolution. *The American Naturalist
496* **86**: 33–44.
- 497 Stropp J, Ladle RJ, M. Malhado AC, Hortal J, Gaffuri J, H. Temperley W, Olav Skøien J,
498 Mayaux P. **2016**. Mapping ignorance: 300 years of collecting flowering plants in

- 499 africa. *Global Ecology and Biogeography* **25**: 1085–1096.
- 500 501 Tank DC, Olmstead RG. **2008**. From annuals to perennials: Phylogeny of subtribe
castillejinae (orobanchaceae). *American Journal of Botany* **95**: 608–625.
- 502 503 Thiers B. **2016**. Index herbariorum: A global directory of public herbaria and associated
staff. New york botanical garden’s virtual herbarium. <http://sweetgum.nybg.org/ih>.
- 504 505 Václavík T, Beckmann M, Cord AF, Bindewald AM. **2017**. Effects of uv-b radiation on
leaf hair traits of invasive plants—combining historical herbarium records with novel
506 remote sensing data. *PloS one* **12**: e0175671.
- 507 508 Verboom GA, Linder HP, Stock WD. **2004**. Testing the adaptive nature of radiation:
Growth form and life history divergence in the african grass genus ehrharta (poaceae:
509 Ehrhartoideae). *American Journal of Botany* **91**: 1364–1370.
- 510 511 Willis CG, Ellwood ER, Primack RB, Davis CC, Pearson KD, Gallinat AS, Yost JM,
Nelson G, Mazer SJ, Rossington NL *et al.* **2017**. Old plants, new tricks:
512 Phenological research using herbarium specimens. *Trends in ecology & evolution* **32**:
513 531–546.
- 514 515 Wolf A, Zimmerman NB, Anderegg WR, Busby PE, Christensen J. **2016**. Altitudinal shifts
of the native and introduced flora of c alifornia in the context of 20th-century
516 warming. *Global ecology and biogeography* **25**: 418–429.

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Supplement518 **Images used.** <https://www.gbif.org/occurrence/1099023487>519 <https://www.gbif.org/occurrence/1057389408>520 <https://www.gbif.org/occurrence/1099023562>521 <https://www.gbif.org/occurrence/1099023490>522 **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.

Table S2

Analysis of variance (ANOVA) to compare drought frequency as a function of life history, season, and their interaction while including species as a random effect.

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

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

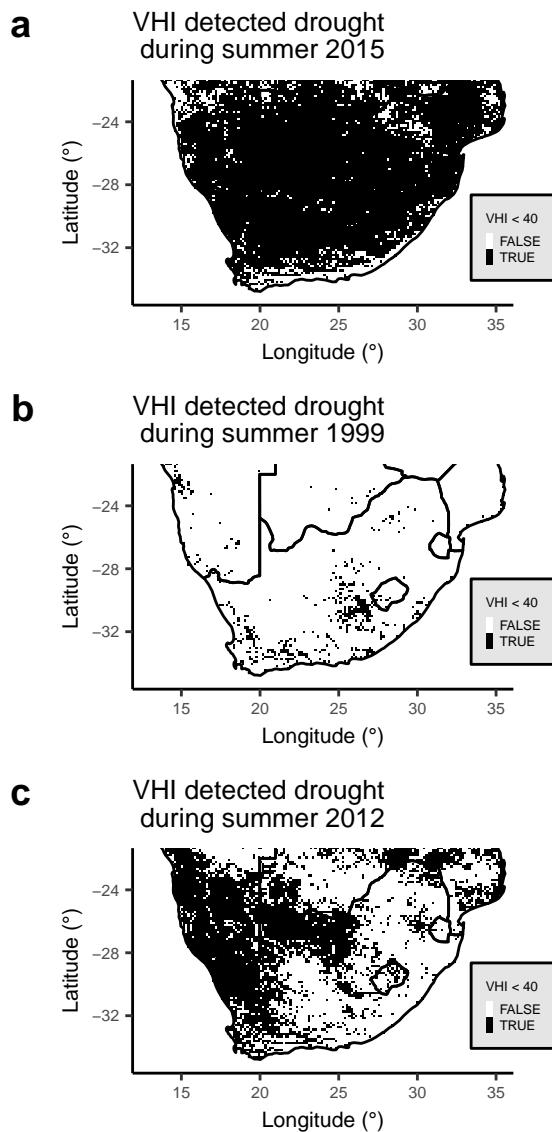


Figure S1. Example years experiencing contrasting degrees of drought in southern Africa. Vegetative Health Index (VHI) values below 40 indicate remotely sensed drought. Drought detection during these years is validated by previously reported precipitation based estimates of drought occurrence (Monyela, 2017) which confirm that while (a) 2015 was one of the worst drought years on record, (b) 1999 was one of the wettest, and (c) 2012 was typical in terms of precipitation patterns. It is worth noting that drought can be detected using the VHI across ecosystems, including those inhabited by perennial rather than annual *Heliophila* species.

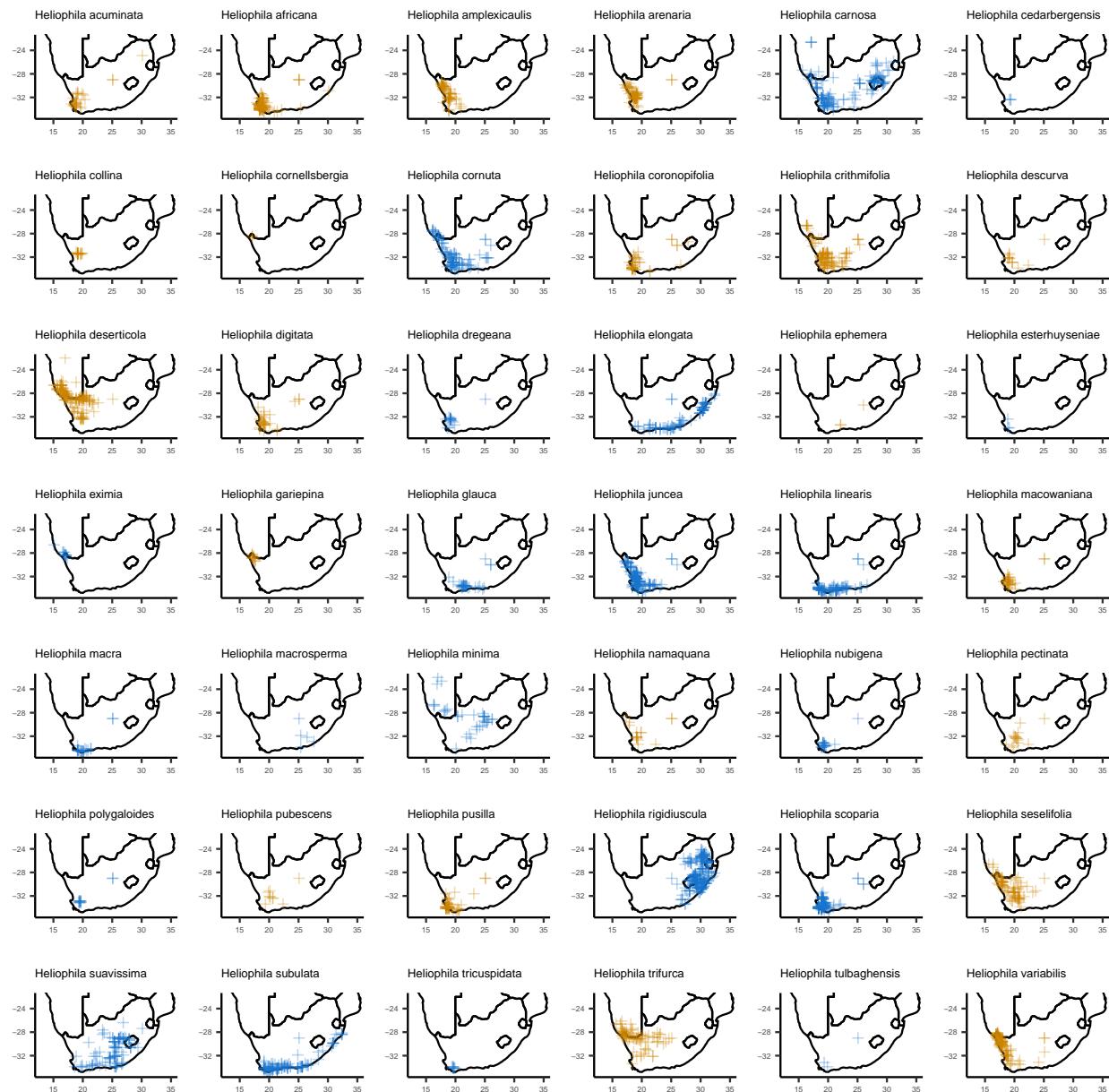


Figure S2. Maps of occurrence records for individual species. Orange points indicate annual species. Blue points indicate perennial species.