

<sup>1</sup> Drought frequency predicts life history strategies in *Heliophila*

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## Abstract

12

## Summary

13       Explaining variation in life history strategies is an enduring goal of evolutionary  
14   biology and ecology. For plants, annual and perennial life histories have long been thought to  
15   reflect adaptation to environments that experience alternative drought regimes. Nevertheless,  
16   empirical support for this hypothesis from phylogeographic analyses remains lacking.

17       Here, we tested classic life history theory in *Heliophila* (Brassicaceae), a diverse genus  
18   of flowering plants native to Africa, with a phylogenetically constrained analysis integrating  
19   34 years of satellite-based drought detection with 2192 herbaria occurrence records.

20       We found that annual and perennial life histories have evolved multiple times in  
21   *Heliophila* and that compared to annuals, perennial species occur in environments where  
22   droughts are significantly less frequent. We also report evidence that annual plants adapt to  
23   predictable drought regimes by escaping drought prone seasons as seeds.

24       These results provide compelling support for longstanding theoretical predictions and a  
25   more nuanced understanding of life history evolution. More broadly, this work outlines a  
26   scalable framework integrating herbaria records and remote sensing to address outstanding  
27   questions in evolutionary ecology.

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

30 Drought frequency predicts life history strategies in *Heliophila*

31 **Introduction**

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

46 Classical theory predicts shorter life spans in environments where adult mortality is  
47 high (Charnov & Schaffer, 1973; Stearns, 1992; Franco & Silvertown, 1996). Because lack of  
48 water is perhaps the greatest threat to survival during vegetative or reproductive growth in  
49 plants, this theory has been extended to the hypothesis that annuality is adaptive when it  
50 allows plants to escape drought (Schaffer & Gadgil, 1975). Indeed, adaptation to drought,  
51 defined as episodes of increased aridity causing plant stress (Passioura, 1996), is often  
52 invoked as an explanation for the success of annual species. And while a few cases are cited  
53 where annuality appears to be more common in environments with greater aridity (Stebbins  
54 Jr, 1952; Morishima *et al.*, 1984), this hypothesis has yet to be supported in a phylogenetic

55 context. In one previous study where this question was addressed phylogenetically, (Evans *et*  
56 *al.*, 2005) annuals were not found to be associated with environments that experience more  
57 drought. This could be explained by the relatively small number of species studied and the  
58 reliance on a limited number of weather stations to characterize environments, highlighting  
59 the need to develop more scalable methods to study trait evolution phylogeographically.

60 It is also critical to consider another dimension of drought adaptation: the expectation  
61 that annuality is most adaptive when droughts are not only frequent but also predictable.  
62 That is, when the frequency of drought is particularly high during certain seasons. Such  
63 predictability is important for selection to lead to escape from those seasons which are  
64 particularly drought prone. While there has been at least one example of annuality  
65 associated with environments qualitatively classified as “predictable” in a general sense  
66 (Datson *et al.*, 2008), the seasonal predictability of drought experienced by annuals has yet  
67 to be rigorously studied. As such, further empirical work is needed to support the model of  
68 annuality as a mechanism of drought adaptation via escape from drought prone seasons.

69 In addition to drought escape in annuals as a mechanism of adaptation to frequent  
70 predictable droughts, droughts may be necessary for the success of annuals more generally by  
71 acting as episodes of disturbance that provide opportunities for annuals to establish and  
72 compete with sympatric perennial species. Indeed, there is considerable evidence that  
73 perennials dominate in environments where disturbance events are infrequent (Rees & Long,  
74 1992; Corbin & D’Antonio, 2004; Clary, 2012). The resulting prediction from this hypothesis  
75 is that in the absence of frequent drought, perenniability should evolve. However, little is  
76 known about this component of life history evolution because previous work has largely  
77 focused on the origins of annuality rather than perenniability (Friedman & Rubin, 2015).

78 Here we combine a long-term global dataset of satellite detected drought events with  
79 metadata from natural history collections to test these classic hypotheses within the African  
80 endemic mustard genus, *Heliophila* L. (Brassicaceae). If annuality is an adaptive strategy

allowing plants to escape drought prone seasons, then drought frequency should predict the distribution of life history strategies across landscapes, and annual species should be more commonly associated with drought prone regions than perennial species. Additionally, if perenniability offers competitive advantage in the absence of drought, associations between life history and drought frequency should be significant even if phylogenies are enriched for transitions from annual to perennial life history strategy. Finally, if annual species have adapted to escape predictably drought prone seasons, observations of growing annual species (i.e. occurring in forms other than seed) should be rare during seasons when drought frequency is highest. Phylogenetic relatedness can influence tests of associations between species' traits and their environments (Felsenstein, 1985; Barrett *et al.*, 1996). Therefore we assessed the relationship between life history distribution and drought frequency in a phylogenetic context.

93

## Materials and Methods

94 **Data**

95 **Data availability.** All analyses were performed using R. All data and the source  
96 code to produce this manuscript are available at <https://github.com/greymonroe/heliophila>.  
97 Software used is listed in the supplement.

98 **Life history data for *Heliophila*.** *Heliophila* is a genus of flowering plants endemic  
99 to the southern Africa including the Cape Floristic and Succulent Karoo Regions. These are  
100 among the most botanically diverse environments on Earth and the *Heliophila* species  
101 occurring there are considered to make up the most diverse genus of the family Brassicaceae  
102 (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). This genus includes both perennial (n  
103 = 21) and annual (n = 21) species and this change in life history strategy has likely arisen  
104 multiple independent times (Appel & Al-Shehbaz, 1997; Mummenhoff *et al.*, 2005).

105 Furthermore, the fine scale climatic heterogeneity of Southern Africa is ideal for studying the  
106 distribution of traits in relation to environmental parameters (Sayre *et al.*, 2013). We used  
107 life histories reported by Mummenhoff *et al.* (2005), grouping species with annual or  
108 perennial life histories. Perenniality was defined based any form of perennial life history (e.g.,  
109 herbs, shrubs, mixed, etc). Because the nature of species reported with mixed traits were  
110 unknown (i.e. plasticity vs. genetic variation), we classified these species here as perennial  
111 since they can maintain vegetative growth after reproduction at least to some capacity.

112 **Heliophila occurrence records.** To characterize the distributions of annual and  
113 perennial *Heliophila* species, all (8670) records for the genus *Heliophila* were downloaded  
114 from the Global Biodiversity Information Facility (gbif.org) on July 21, 2018 (GBIF, 2018).  
115 herbaria records such as these provide a rich data sources to characterize the  
116 geographical distributions of species (Thiers, 2016; Willis *et al.*, 2017; Lang *et al.*, 2018).  
117 And as they become digitized (Soltis, 2017), these collections have been used to study  
118 relationships between trait distributions, geography, and climate (Davis *et al.*, 2015; Stropp  
119 *et al.*, 2016; Wolf *et al.*, 2016; Václavík *et al.*, 2017).

120 **Sequence data for phylogeny.** An alignment of ITS I and II sequences for 21  
121 annual and 21 perennial *Heliophila* species was obtained from the authors of Mandáková *et*  
122 *al.* (2012). Individual ITS I and II sequences for *Aethionema grandiflorum*, *Alliaria petiolata*,  
123 *Cardamine matthioli*, *Chamira circaeoides*, and *Rorippa amphibia* were downloaded from  
124 Genbank.

125 **Satellite-detected drought data.** Remotely sensed data is a powerful tool for  
126 characterizing seasonal patterns in drought because it is less limited in spatial and temporal  
127 scope and resolution than weather stations or field observations (AghaKouchak *et al.*, 2015).  
128 From an ecological perspective, droughts are best defined as episodes of plant stress caused  
129 by elevated aridity (Passioura, 1996). Thus remote sensing offers the additional benefit for  
130 studying drought as an agent of natural selection because plant stress caused by drought can

131 be observed from space (Kogan, 1995a). The remotely sensed Vegetative Health Index (VHI)  
 132 is one such metric, which detects landscape scale reductions in plant cover and temperature  
 133 conditions characteristic of drought (Kogan, 2001). Generated from data collected by NOAA  
 134 AVHRR satellites since 1981, the VHI is a composite index combining Normalized Difference  
 135 Vegetation Index (NDVI) derived quantification of vegetative stress (Vegetative Condition  
 136 Index - VCI) with temperature stress indicated by anomalies in thermal spectra  
 137 (Temperature Condition Index - TCI). These indicies were developed to create an unbiased  
 138 quantification of drought across ecosystem types. The VHI of year  $y$  during week  $w$  of [1, 52]  
 139 at pixel  $i$  is derived from the following equations, where  $n$  is the number of years observed.

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

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

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

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

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

145 By combining VCI and TCI, the VHI is distinguishes drought from other forms of vegetative  
 146 stress (Kogan, 1995b). The use of the VHI to detect drought has been validated globally and  
 147 across ecosystem types (AghaKouchak *et al.*, 2015), including in southern Africa, the focal  
 148 region of this study (Figure S1). To date, the VHI has most often been applied for  
 149 evaluating drought risk for agricultural research (e.g., Rojas *et al.*, 2011; Kogan *et al.*, 2016).

150 But it also presents a tool to study seasonal patterns in the frequency of drought across  
151 environments and to test hypotheses about the effect of drought on ecological and  
152 evolutionary processes (Kerr & Ostrovsky, 2003). As such, the VHI has been applied recently  
153 to study drought related ecology of natural species and proven useful for predicting  
154 intraspecific variation in drought tolerance traits and genes (Mojica *et al.*, 2016; Dittberner  
155 *et al.*, 2018; Monroe *et al.*, 2018b). Here, we accessed VHI data at  $16\text{km}^2$  resolution from  
156 1981 to 2015 ([https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh\\_ftp.php](https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php)) to  
157 characterize the seasonal drought frequencies experienced by annual and perennial *Heliphila*  
158 species across their native range of southern Africa.

159 **Analyses**

160 **Drought frequency calculations.** To characterize drought regimens across the  
161 distributions of annual and perennial species of *Heliphila*, we calculated drought during  
162 different seasons at the location of observations for *Heliphila* records using the VHI.  
163 Specifically, we created global maps of the frequencies of observing drought conditions  
164 between years (VHI $<40$ , NOAA) during the winter (quarter surrounding winter solstice),  
165 spring (quarter surrounding spring equinox), summer (quarter surrounding summer solstice)  
166 and fall (quarter surrounding fall equinox) from 1981 to 2015. From these maps, the drought  
167 frequency during the winter, spring, summer, and fall were extracted for the locations of all  
168 GBIF records.

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

- 171 • records for species with reported life history  
172 • records with geospatial data  
173 • records without known geospatial coordinate issues (i.e., coordinates reported are those

174 of herbarium)

- 175 • records from collection sites classified as land pixels in the VHI dataset
- 176 • records from Africa (to exclude locations of cultivation)
- 177 • records without duplicates (i.e., identical species, location, collection date)

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

179 *Aethionema grandiflorum*, *Alliaria petiolata*, *Cardamine matthioli*, *Chamira circaeoides*, and

180 *Rorippa amphibia*) and ingroup *Heliphila* ITS I and II sequences were aligned using

181 MAFFT (Katoh *et al.*, 2002) with strategy G-INS-I, offset value 0.1, and all other options

182 set as default. The *GTR + Γ* model of nucleotide substitution was determined to best fit the

183 data based on AIC using jModelTest2 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012). A

184 maximum clade credibility tree with branch lengths as relative time was estimated by

185 summarizing data from six runs of 100,000,000 generations of Bayesian Markov chain Monte

186 Carlo conducted in BEAST 2 (Bouckaert *et al.*, 2014). Model selection and phylogenetic

187 analyses were conducted through the CIPRES Science Gateway (Miller *et al.*, 2010).

188 Ancestral state estimation was performed in R using the package phytools (Revell, 2012) to

189 generate 10,000 stochastic character maps simulated under an equal rates model of character

190 evolution for the trait life habit (annual or perennial).

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

192 To evaluate the hypothesis that annual and perennial life history strategies reflect

193 adaptations to alternative drought regimes, we tested the corresponding prediction that the

194 observed distributions of annual and perennial *Heliphila* species would be significantly

195 associated with historic drought frequency. First, we compared the frequency of drought

196 across all occurrence records of between annual and perennial species by t-tests. Independent

197 tests were performed to compare drought frequency between annuals and perennials during

198 each season. We also tested for a relationship between drought frequency and life history,

199 season, and their interaction by an analysis of variance while including species as a random

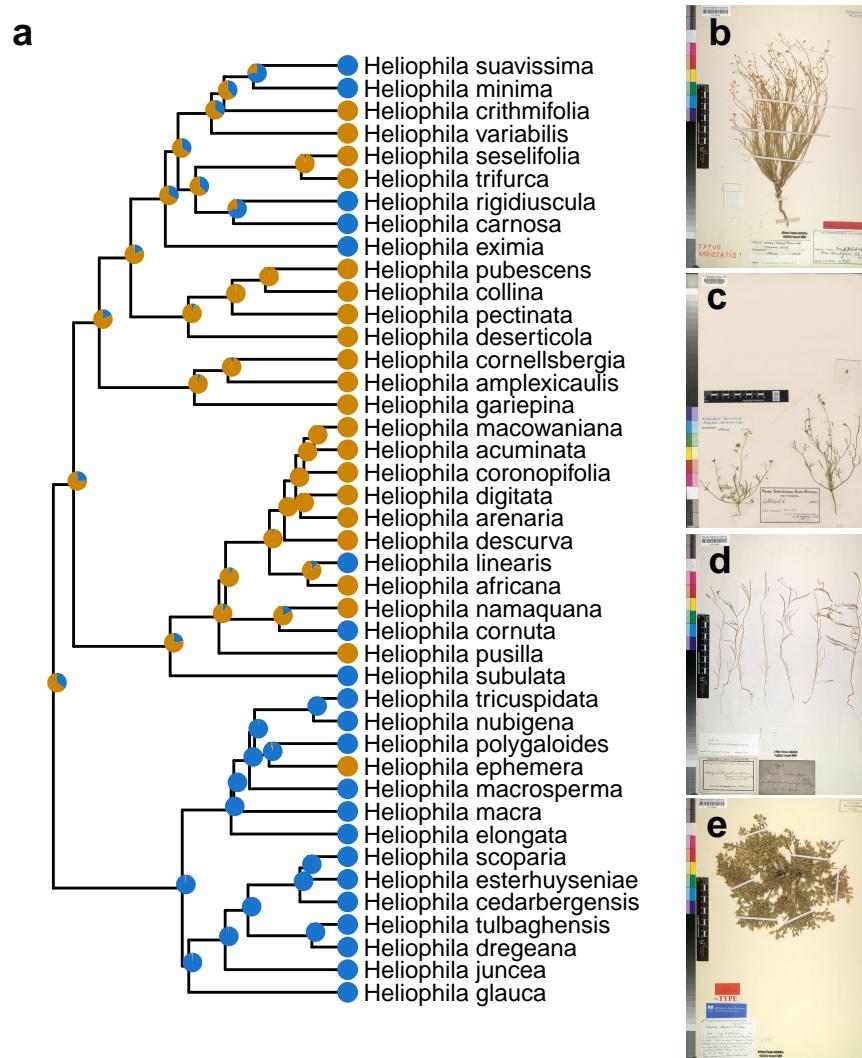
200 effect. To account for variation in the number of occurrence records per species, we next  
201 calculated the mean drought frequency during the winter, spring, summer and fall for each  
202 species. Because shared evolutionary history of closely related species can lead to spurious  
203 associations between traits and environments (Felsenstein, 1985), we tested for a relationship  
204 between life history strategy and drought frequency while controlling for phylogeny using  
205 phylogenetic logistic regression (Ives & Garland, 2010). This statistical approach is designed  
206 to control for the confounding effects of geographic relationships explained by demographic  
207 history rather than processes of natural selection.

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

## 212 Results

213 The *Heliophila* phylogeny was consistent with previous studies (Mummenhoff *et al.*,  
214 2005; Mandáková *et al.*, 2012). Based on 10,000 stochastic character maps simulated under  
215 an equal rates model of character evolution in life history, an average of approximately eight  
216 changes from annual to perennial and five changes from perennial to annual are observed per  
217 stochastic character map (Figure 1a). These results suggest that the ancestral state of  
218 *Heliophila* was annual and that both charcter states have arisen independently mutliple  
219 times.

220 Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history  
221 (Mummenhoff *et al.*, 2005), 2856 had geospatial data, 2833 did not have geospatial issues,  
222 2684 were located on pixels classified as land having drought measurements, 2543 were  
223 located in Africa, 2192 were not duplicated. Thus, after all filtering steps, 2192 records for



*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 (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.

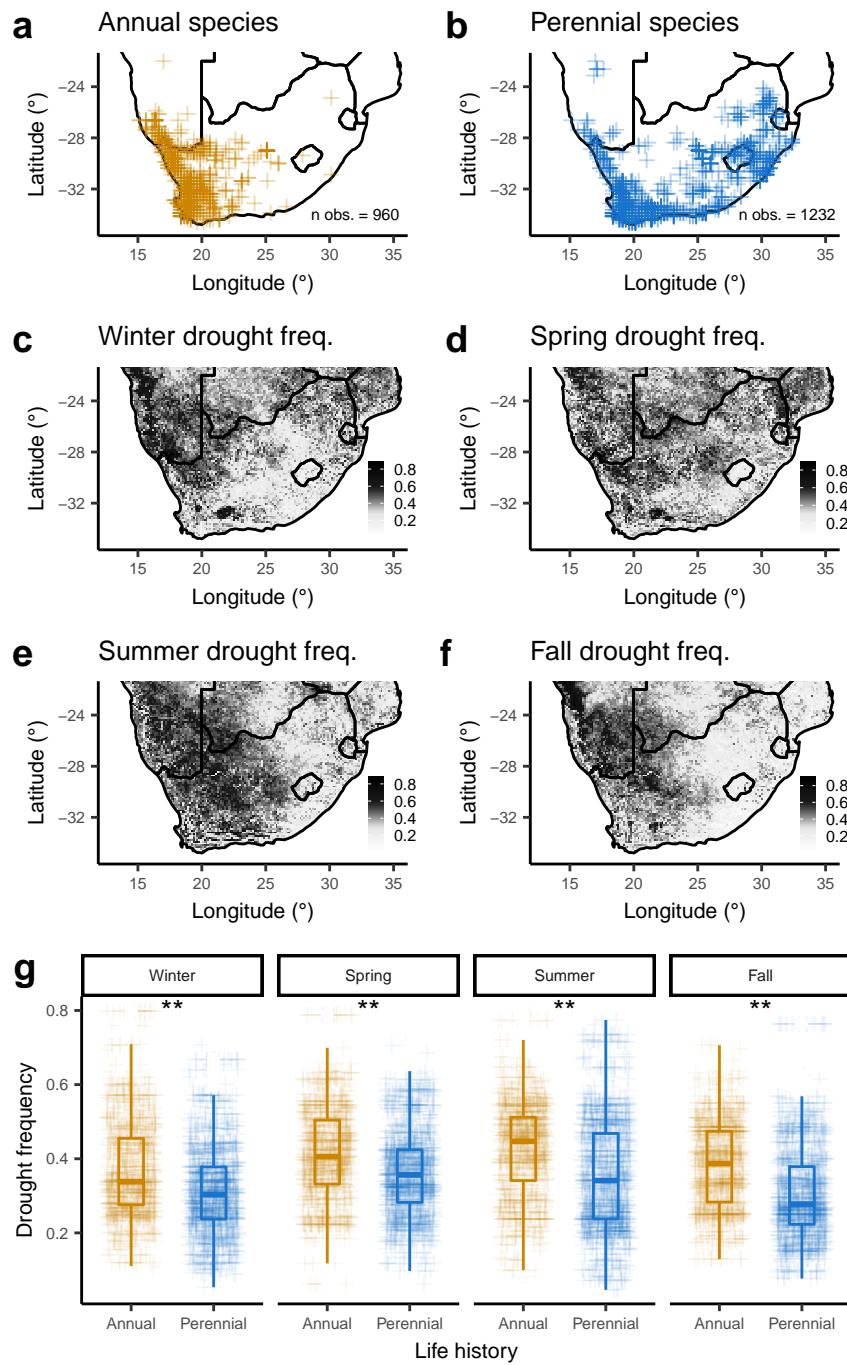


Figure 2. Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) fall detected using the VHI. (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (t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

224 42 species (Figure 1, Table S2) passed for further analyses. The number of samples varied  
225 between species, with a mean of 52.19 samples per species. *H. rigidiuscula* had the most  
226 records, 201, and *H. cornellsbergia* the fewest, 2 (Table S2).

227 There were clear visual differences between the distributions of the 960 annual and the  
228 1232 perennial *Heliphila* observation records (see Figure S2 for maps of individual species).  
229 While annual species were generally found in the western regions of South Africa and  
230 Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Figure 2a), the  
231 occurrence of perennials extended to the southern and eastern coast of South Africa (Figure  
232 2b).

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

241 We found that the frequency of drought was significantly higher at the locations of  
242 occurrence records for annual species. When comparing across all occurrence records (all  
243 records rather than species means, Figure 2g), the frequency of drought was significantly  
244 higher at the location of annuals during the winter ( $t = 10.65$ ,  $p < 0.01$ ), spring ( $t = 10.73$ ,  
245  $p < 0.01$ ), summer ( $t = 12.67$ ,  $p = < 0.01$ ), and fall ( $t = 15.26$ ,  $p < 0.01$ ). A mixed-model  
246 analysis of variance which included species as random effect also identified a significant  
247 relationship between drought frequency and life history ( $p < 0.01$ ), season ( $p < 0.01$ ) and  
248 their interaction ( $p < 0.01$ ) (Table S1). Because a comparison across all occurrence records  
249 does not account for variation in the number of records per species (Table S2) or species

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.

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 demographic history 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

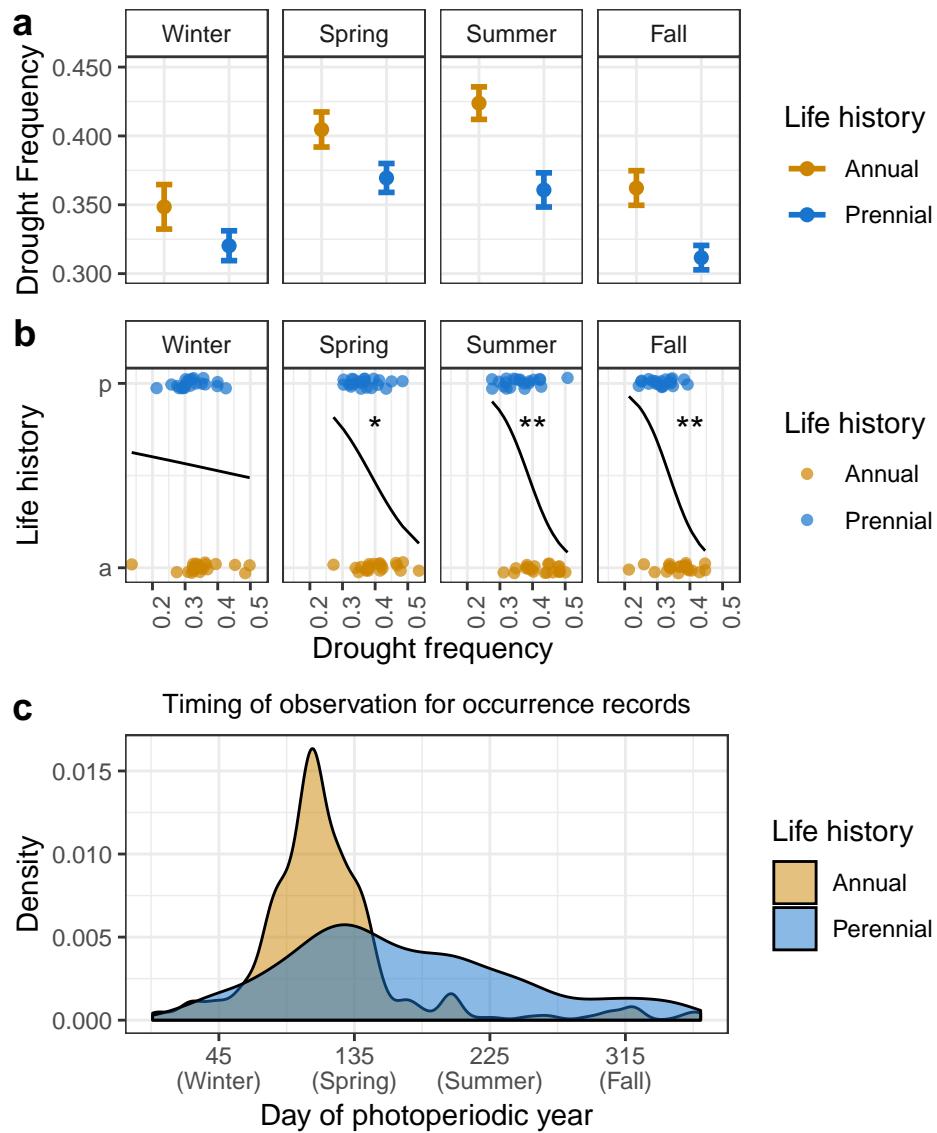


Figure 3. (a) Comparison (mean + SE) of drought frequency across seasons calculated at the occurrence locations of GBIF records of annual and perennial species of *Heliophila*. (b) Results from phylogenetic logistic regression, where the line shows the model fit and \* =  $p < 0.05$ , \*\* =  $p < 0.01$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

258 history theory hypothesizes that annuality reflects adaptation to such environments because  
 259 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 ( $\text{ks.test } D = 0.25, p < 0.01$ ;  $\text{bartlett.test } K2 = 503.18, p < 0.01$ ) This is consistent with a model of life history in which annual species flower in the spring, set seed, senesce, and die before the summer. Thus, these annual species are likely to remain dormant during the summer and fall, when drought is the strongest predictor of the distributions of annual and perennial life histories (Figure 3a).

## Discussion

To test the hypothesis that annual and perennial plants reflect adaptation to alternative drought environments we examined the landscape distribution of life history strategies in the large and diverse mustard genus, *Heliophila*. Using metadata of 2192 occurrence records and a 34 year dataset of satellite-detected droughts, we tested the prediction that annual species are more often observed in drought-prone locations than perennial species, when controlling for phylogenetic relatedness. We found that drought frequency is significantly different between the distributions of annual and perennial species, with annuals being found in environments with more frequent drought, and that this signal is strongest during the seasons when annuals are likely escaping via seed dormancy. These results remain significant while controlling for the phylogenetic relationships of *Heliophila* species, yielding support for the role that natural selection has played in driving contemporary distributions of these alternatives strategies in relation to drought regimens.

We cannot eliminate the possibility that confounding traits or environmental variables

285 are the causative factors explaining variation in the distributions of annual and perennial  
286 species. Nevertheless, these results provide quantitative support for the classic prediction  
287 that annual species are found in environments that experience more frequent drought than  
288 perennial species. These findings are a valuable contribution to previous investigations of  
289 associations between life history and climate (Morishima *et al.*, 1984; Evans *et al.*, 2005;  
290 Datson *et al.*, 2008; Cruz-Mazo *et al.*, 2009). To our knowledge this is the first study to  
291 demonstrate a significant association between life history and drought in a phylogenetic  
292 context informed by large scale species distribution data and long term drought detection.

293        Unfortunately, herbarium collections and their associated data do not represent  
294 systematic or random sampling of a species distribution. Significant biases in collecting exist,  
295 which we have not necessarily controlled for here, and may have some effect on our findings,  
296 such as a bias toward collecting near roads or near the locations of natural history collections  
297 (Daru *et al.*, 2018). Future research will benefit from systematic sampling efforts to avoid  
298 these noted biases. However, the ecosystems of southern Africa include several biodiversity  
299 hotspots and are among the most botanically well sampled regions on Earth (Daru *et al.*,  
300 2018), suggesting that this may currently be the optimal region for our analyses of life  
301 history distribution. Indeed, we were able to use 2192 occurrence records to study 42 species,  
302 which represents a significant advance over relying on personal observations to characterize  
303 species distributions.

304        These findings empirical provide support classical theoretical predictions about the  
305 adaptive value of annual and perennial life history strategies. Taken together, they suggest  
306 that in *Helichrysum*, annual species are adapted to environments with increased summer  
307 droughts by avoiding these seasons in a dormant seed phase of their life cycle. They also  
308 suggest that perenniability is adaptive in environments where droughts are less frequent.  
309 While most previous work has focused on describing the evolutionary origins of annuality  
310 (Barrett *et al.*, 1996; Conti *et al.*, 1999; Andreasen & Baldwin, 2001; Verboom *et al.*, 2004;

311 Friedman & Rubin, 2015) there are at least a few other cases where perenniability appears to  
312 have arisen from an annual ancestor (Bena *et al.*, 1998; Tank & Olmstead, 2008). And while  
313 early theory predicted selection for annuality when adult mortality is high (Stearns, 1992),  
314 we also find evidence that perenniability could be explained by reduced frequency of drought.  
315 This is supported by the theoretical prediction that perenniability is advantageous in stable  
316 habitats. The phylogeny reveals several transitions from annual to perennial life history  
317 (Figure 1a) and the distributions of perennial *Heliophila* extend into regions where drought  
318 frequency is low (Figure 2b, Figure S2). Perennials may be able to out compete annual  
319 relatives in environments where the infrequency of drought favors strategies that allow plants  
320 to benefit from growth over many seasons. This also suggests that annuals rely on drought  
321 as a source of disturbance for seedling recruitment when competing with perennials (Corbin  
322 & D'Antonio, 2004). Indeed, no annual species were observed in the low drought regions of  
323 eastern South Africa (Figure 2, Figure S2).

324 These findings suggest that species with locally adaptive life history strategies could be  
325 threatened by rapidly changing drought regimens (Dai, 2011). In light of the findings here,  
326 changes in eastern South Africa which is forecast to experience significantly lower rainfall  
327 (Service & Comission, 2017) could be particularly impactful. In this study we found that this  
328 region is currently dominated by derived perennial species of *Heliophila*. However, if drought  
329 become more frequent in this region, it may allow for the establishment of annuals. Such  
330 changes in selection patterns and shifts in plant functional diversity could have impacts on  
331 ecosystem functioning and processes such as carbon cycling (Garnier *et al.*, 1997; Roumet *et*  
332 *al.*, 2006; Monroe *et al.*, 2018a). Furthermore, the changes in frequency of drought may be  
333 an important factor when considering the use of perennial cropping systems (Parry *et al.*,  
334 2005; Lelièvre & Volaire, 2009).

335 In conclusion, we find strong support for classic life history theory which predicts that  
336 annuality is adaptive in environments where droughts occur more frequently. Additionally,

337 we report evidence consistent with a life history model in annuals in which they escape  
338 drought prone seasons during the seed phase of their life cycle. Finally, we find evidence that  
339 the distributions of perennial lineages may indicate a competitive advantage in areas where  
340 droughts are infrequent. More broadly, this work highlights the irreplaceable value of natural  
341 history collections and demonstrates the power of combining such information with large  
342 scale remote sensing data to address outstanding classic hypotheses in ecology and evolution.

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347 **Author contributions**

348 JGM, BG, KGT and JKM contributed to the design of the research, interpretation,  
349 and writing the manuscript. JGM, BG, and KGT contributed to the performance of the  
350 research and data analysis.

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**Supplement**506      **Images used.**    <https://www.gbif.org/occurrence/1099023487>507      <https://www.gbif.org/occurrence/1057389408>508      <https://www.gbif.org/occurrence/1099023562>509      <https://www.gbif.org/occurrence/1099023490>510      **Supplementary tables and figures.**

Table S1

*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	numDF	denDF	F.value	p.value
intercept	1	8,720.0000	2,833.9567	0.0000
life history	1	40.0000	12.2117	0.0012
season	3	8,720.0000	106.4947	0.0000
life history x season	3	8,720.0000	4.8301	0.0023

Table S2

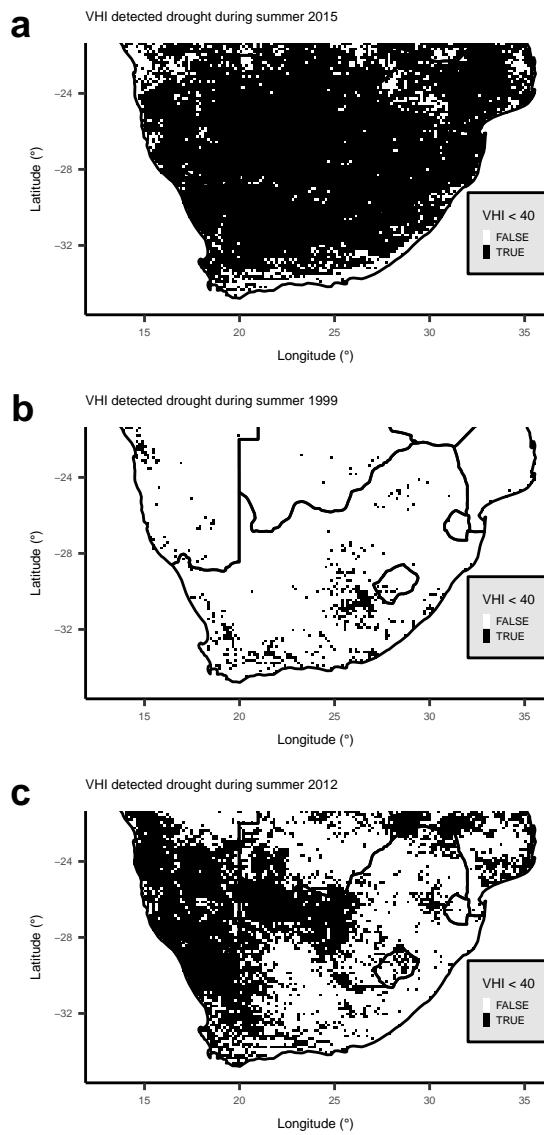
*Heliophila species records and the mean drought frequencies during different seasons at the location of records*

Species	LH	n	Winter	Spring	Summer	Fall
Heliophila acuminata	a	28	0.32	0.38	0.41	0.36
Heliophila africana	a	91	0.33	0.35	0.34	0.34
Heliophila amplexicaulis	a	60	0.32	0.36	0.39	0.33
Heliophila arenaria	a	65	0.34	0.37	0.38	0.34
Heliophila carnosa	p	129	0.33	0.37	0.39	0.31
Heliophila cedarbergensis	p	3	0.40	0.43	0.32	0.27
Heliophila collina	a	16	0.35	0.47	0.48	0.45
Heliophila cornellsbergia	a	2	0.33	0.42	0.35	0.21
Heliophila cornuta	p	101	0.35	0.40	0.40	0.34
Heliophila coronopifolia	a	40	0.37	0.42	0.40	0.37
Heliophila crithmifolia	a	97	0.35	0.42	0.45	0.38
Heliophila descurva	a	12	0.36	0.38	0.38	0.29
Heliophila deserticola	a	133	0.48	0.48	0.46	0.45

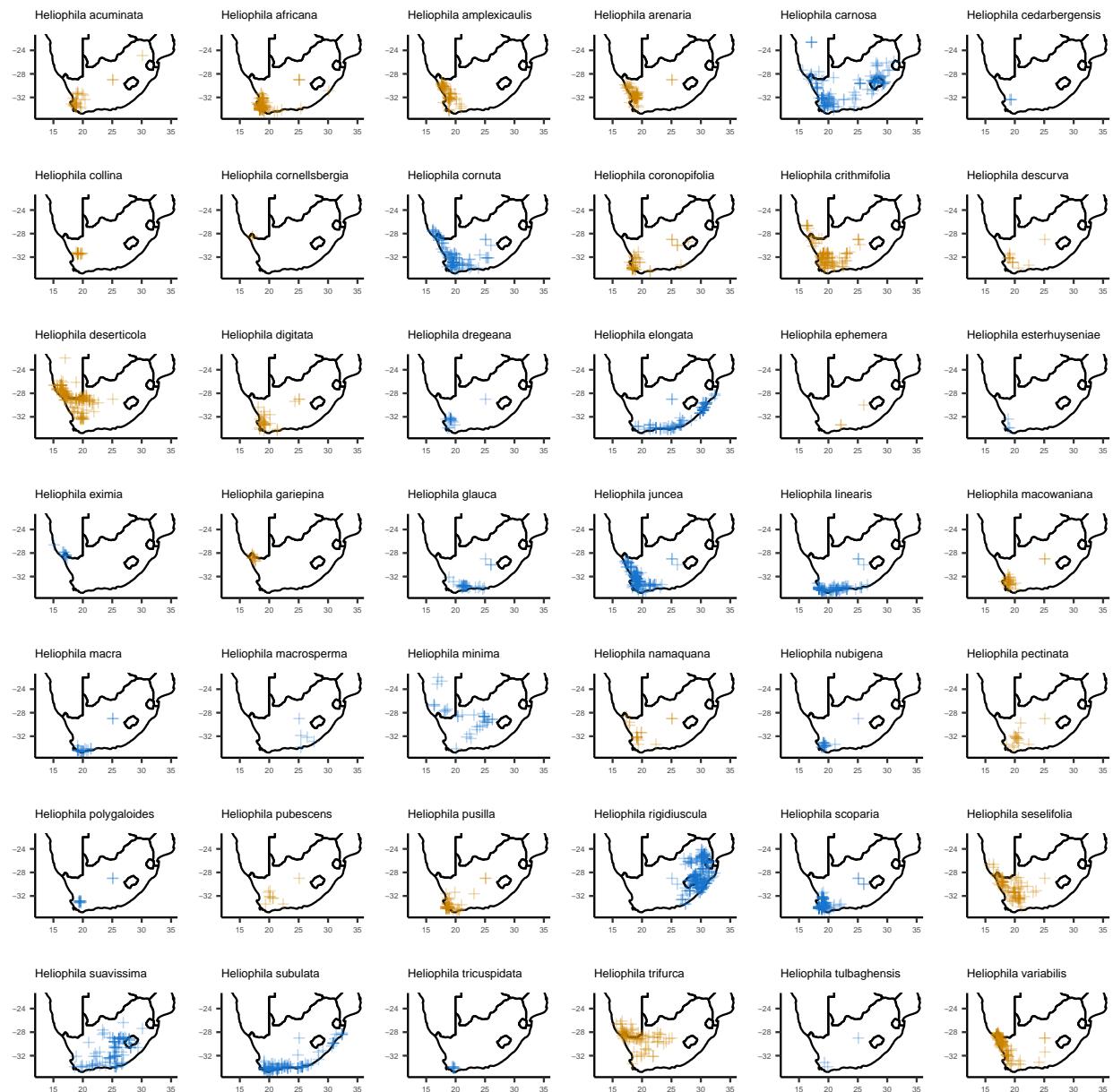
<i>Heliophila digitata</i>	a	30	0.33	0.38	0.44	0.38
<i>Heliophila dregeana</i>	p	17	0.33	0.37	0.33	0.32
<i>Heliophila elongata</i>	p	82	0.26	0.32	0.30	0.25
<i>Heliophila ephemera</i>	a	3	0.14	0.27	0.31	0.26
<i>Heliophila esterhuyseniae</i>	p	3	0.21	0.30	0.37	0.27
<i>Heliophila eximia</i>	p	12	0.42	0.41	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>Helophilus variabilis</i>	a	97	0.35	0.41	0.40	0.37
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*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.* Example years experiencing contrasting degrees of drought in southern Africa. Vegetative Health Index (VHI) values below 40 indicate remotely sensed drought. Drought detection during this years is validated by precipitation based estimates of drought occurrence (Standardized Precipitation Index) 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 (Monyela, 2017). 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.