

1 Plant life history strategies predicted by satellite-detected drought

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Abstract

Identifying the environmental factors that predict the evolution of annual and perennial life history strategies in plants is important for understanding ecosystem functioning, perennial cropping systems, and is a long-standing goal of evolutionary ecology. A classic hypothesis is that annual and perennial strategies reflect adaptation to environments that differ in relative drought frequency. We test this hypothesis in *Heliophila* (Brassicaceae), a genus of flowering plants native to Southern Africa using herbarium occurrence records and satellite-detected drought histories. We find that perennial *Heliophila* species are observed in environments where droughts are significantly less frequent compared to annuals, especially with regards to summer drought. These correlations remain predictive while controlling for phylogeny, lending support to the hypothesis that drought associated natural selection has shaped differences in the distributions of these strategies. Additionally, the collection dates of herbarium records are consistent with a scenario in which annual species escape drought prone seasons. Together these results point to a model of evolution that supports classical hypotheses favoring perenniality in environments that experience less drought, compared to annuals which escape drought prone seasons as seed. Thus, changing drought regimens during the Anthropocene may threaten locally adapted species.

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

Word count:

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Introduction

Life history

Plants exhibit extraordinary diversity in life history strategies, from herbaceous species that complete the entire seed to seed life cycle in a number of weeks {Guo, 2012 #73} to trees that live for thousands of years {Brown 1996 <http://www.rmtrr.org/oldlist.htm> }. Along this continuum an important division exists, distinguishing annuals which complete their seed to seed life cycle within a single calendar year from perennials which can persist over multiple years and therefore experience the entire range of seasonal conditions. The ecological factors that explain the evolution of these alternative strategies remains poorly resolved {Friedman, 2015 #523}. Understanding the drivers of selection for these alternative strategies is important because annuals and perennials have differing impacts on ecosystem functioning, such as higher nitrogen concentration in perennials and larger specific root length in annuals that affect nutrient cycling {Garnier, 1997 #280}{Roumet, 2006 #738}. Furthermore, predicting the conditions that favor these strategies in nature is useful for developing more sustainable perennial cropping systems {Lelievre and Volaire, 2009}.

Hypotheses

Seasonal drought conditions can represent a severe challenge to the persistence of individual organisms. Well-established hypotheses suggest that an annual life history is adaptive in environments where frequent droughts makes an escape from stressful drought conditions in the form of seed advantageous {Stearns 1992}{Silvertown and Charlesworth, 2001}. These hypotheses are based on models of life history evolution in which short life cycles are favored in unpredictable environments or those with frequent stressful conditions.

Plants are expected to be more likely to survive a drought that cooccurs with the seed phase of a plant's life cycle in which they are most resistant to desiccation. Previous efforts to address this hypothesis have yielded mixed or qualitative results. Transitions to annuality in *Oenothera* were associated with warmer summers and drier winters, but not with increased drought directly {Evans, 2005 #260}. Annual and perennial species of *Nemesia* were qualitatively associated with winter rather and summer rainfall environments respectively {Datson, 2008}. Similarly, annual species of *Scorzoneroideae* were associated with environments classified as "unpredictable" {Cruz-Mazo, 2009 #598}. Annual and perennial varieties of the wild rice species *Oryza rufipogon* were observed more frequently in dry and humid climates, respectively {Morishima et al. 1984}. While these reports suggest the prominence of annuals in environments considered more arid, a quantitative assessment of how historic drought frequency may favor annual or perennial life history strategies remains lacking.

Summary

Here we combine a long-term dataset of global imaging with metadata from natural history collections to test classic hypotheses about the evolution of life history strategies within the African endemic mustard genus, *Heliophila* L. (Brassicaceae). If annual species temporally escape drought as seed, then drought frequency should be an important determinant of the distribution of life history strategies across the landscape, and annual species should be more commonly associated with drought prone regions than perennial species. Furthermore, if annual species have adapted to escape drought prone seasons as seeds, observations of annual species should be rare during drought prone seasons. Phylogenetic relatedness can have significant non-random effects on species distributions and life history traits (cite), and therefore we assessed the relationship between life history distribution and drought frequency in a phylogenetically controlled background.

Methods

Data

Drought. Remotely sensed data is a valuable tool for characterizing seasonal patterns in drought {AghaKouchak 2015}. With these data, we can exploit the fact that satellite imagery can detect reductions in plant cover and moisture at landscape scales that are characteristic of drought conditions. Unlike weather station data, which is limited in geographic coverage, and manual observation, which is limited in scope, satellite detected data provides a long term global historical record of drought events at fine temporal and spatial resolutions. One such measure, the Vegetative Health Index (VHI), has been collected since 1981 by NOAA AVHRR satellites and is a combined measure of thermal and vegetative parameters. VHI quantifies drought induced vegetative stress weekly by detecting reduced plant cover based on the normalized difference vegetation index (Vegetative Condition Index) combined with reductions in moisture associated with anomalies in thermal spectra (Temperature Condition Index). Put most simply, the VHI detects drought by identifying environments that appear unusually brown and dry for that location and time of the year.

This data provides a global, long term, and quantitative perspective on drought variability. The VHI database (see methods) presents a valuable resource to study seasonal patterns in the frequency of drought across environments and to test hypotheses about the effect of drought on ecological and evolutionary processes. As such, it has been validated as a tool for detecting drought and predicting crop yields {Kogan 1997}. It has also proven useful for predicting infraspecific variation in drought tolerance traits and genes {Mojica et al 2016}{Dittberner et al 2018}{Monroe et al 2018}.

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(Temperature Condition Index). Put most simply, the VHI detects drought by identifying environments that appear unusually brown and dry for that location and time of the year.

The Vegetative Health Index (VHI) was used to examine seasonal drought frequency at the collection locations of *Heliophila* herbarium specimens. The VHI is a satellite-detected drought measurement method based on observations of vegetative stress caused by drought {Kogan, 1995 #534}, combining deviations from historic climatic (Temperature Condition Index) and vegetative conditions (Vegetative Condition Index). The VHI has been measured weekly at 16km² spatial resolution since XXXX. The frequencies of observing drought conditions (VHI<40, standard recommended by NOAA developers of VHI) during the southern hemisphere spring (quarter surrounding spring equinox), summer (quarter surrounding summer solstice), fall (quarter surrounding fall equinox), and winter (quarter surrounding winter solstice) were calculated globally from 1981 to 2015. These values were calculated for the collection location of each *Heliophila* herbarium specimen in our filtered dataset.

$$NDVI = (Ch2 - Chl)/(Ch2 + Chl)$$

$$NDVI = \frac{NIR - Red}{NIR + Red}$$

$$VCI = 100 \frac{NDVI - NDVI_{min}}{NDVI_{max} - NDVI_{min}}$$

$$TCI = 100 \frac{T - T_{min}}{T_{max} - T_{min}}$$

$$VHI = 0.5(VCI) + 0.5(TCI)$$

This data provides a global, long term, and quantitative perspective on drought variability. The VHI database presents a valuable resource to study seasonal patterns in the frequency of drought across environments and to test hypotheses about the effect of drought on ecological and evolutionary processes. As such, it has been validated as a tool for detecting drought and predicting crop yields (???). It has also proven useful for predicting infraspecific variation in drought tolerance traits and genes (Dittberner et al., 2018; Mojica et al., 2016; Monroe et al., 2018).

Life history. *Heliophila* is a genus of flowering plants endemic to the southern portion of Africa including the Cape Floristic and Succulent Karoo Regions which are among the most botanically diverse environments on Earth. Indeed, the estimated ~50 *Heliophila* species are considered to represent the most diverse genus of the family Brassicaceae {Mummenhoff, 2005 #494}. 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, 2005 #494}. These multiple transitions between life history strategy and its well documented record in global herbaria provided the ideal system to address classic hypotheses about the evolutionary drivers of annual and perennial life history strategies.

Phylogeny. Herbaria records and satellite detected drought provide data with which the distributions of annual and perennial species can be compared with respect to historic drought frequency. However, it is necessary to control for the demographic history caused by common ancestry of species if evolutionary processes such as natural selection are to be invoked as explanations for any differences observed. If, for example, annual and perennial species show significantly different ranges with respect to historic drought this could be confounded by common ancestry if annuals originated from a common ancestor and vice versa. In this case, it would be challenging to distinguish between natural selection and demographic history. On the other hand, if annual and perennial life history strategies arose

independently in multiple species, controlling for phylogenetic relationships allows us to better account for demography and make stronger assertions about the importance of processes such as natural selection to explain patterns.

Heliophila is a charismatic genus of flowering plants from the Brassicaceae provides a valuable model to study the evolution of annual and perennial life history strategies because each has arisen independently multiple times within the genus. These independent origins allow for phylogenetically constrained analyses comparing the climate distributions of annual and perennial species, to gain greater insight into the role of selection.

Aligned Heliophila ITS sequences were obtained from previous work by Mandáková et al. {Mandáková, 2012 #339}. Aethionema, Alliaria, Cardamine, Chamira, and Rorippa ITS records from were downloaded from Genbank (link) and aligned together with Heliophila ITS sequences using MAFFT as outgroups? (cite). Model selection for construction of phylogeny was performed in jModeltest2 with CIPRES (cite). Based on this analysis, $GTR + L$ were selected. Ultrametric phylogeny was estimated with branch lengths as relative time (details). Life history character states were used based on habit reported by Mummenhoff et al. {Mummenhoff, 2005 #494}. Species reported to have any form of perennial life history (such as biennial...) were classified for analyses here as perennial, where species reported to have strictly annual life histories were classified for analyses here as annual.

Herbarium Specimens. Botanists have collected and maintained over 350 million botanical specimens worldwide over the past 300 years (Lang et al 2018). These collections, housed in herbaria, comprise an enormous, yet largely untapped, ecological dataset. These specimens are increasingly being recognized as an invaluable and underutilized source of data pertaining to biological responses to past environmental conditions (Pyke et al. 2010). Herbarium specimens and their associated metadata have been used since the 1960s to study species' geographical distributions (reviewed in Lang et al. 2018). Herbarium specimens have been used to track plant responses to climate change using herbarium time-series, including

the relationships between traits, geography, and climate. {Wolf et al. 2016, Davis et al. 2015, Stropp et al. 2017}. A potentially fruitful approach combines herbarium data with remotely sensed data sets that characterize the environmental and climatic conditions across landscapes. For example, remotely sensed global ultraviolet-B radiation exposure may explain differences in trichome phenotypes, observed from herbarium specimens, between the native and invasive ranges of two herbaceous plants (Václavík et al. 2017).

Herbarium specimen records for all *Heliophila* species were downloaded from the Global Biodiversity Information Facility (gbif.org) on July 21, 2018. Several filtering steps were employed to clean this data (see Sup Mat. R code). For these analyses, records were restricted to those which are associated with a physical herbarium specimen, rather than other types of observations. Consequentially, this sample represents individuals in a narrow range of vegetative and/or flowering states – for example, herbarium specimens cannot be collected for individuals existing as seed. Analyses were restricted to *Heliophila* species with previously-reported life history information {Mummenhoff, 2005 #494}; 42 of ~50 named species in this genus were used. Only records including geo-referenced information (latitude and longitude of collection site) were used for downstream analyses of historic drought frequency. To discard records likely to be erroneous and to restrict analyses to plants in their native, non-cultivated, habitats, records occurring outside of the native range (roughly, the southern half of Africa) were removed. This excluded specimens such as those growing in likely cultivation in Australia or terrestrial plants recorded from non-terrestrial oceanic locations.. Finally, duplicate records, based on species, collection location coordinates, and date, were removed.

We downloaded 8670 records from GBIF.

Analyses

Drought frequency.

Herbarium clean up. We filtered raw GBIF by restricting our analyses to

- Species with reported life history
- Records with geospatial data
- Records from collection sites classified as land pixels
- Records for perserved specimens
- Records from Africa
- Non-duplicate records (ie. identical species, location, collection date)

Phylogeny.

Contrast. To evaluate the hypothesis that annual and perennial life history strategies reflect adaptations to alternative drought regimes, we tested the corresponding prediction that the observed distributions of annual and perennial *Heliophila* species would be significantly associated with historic drought frequency. To do so, the average drought frequency for each season was calculated across the herbarium specimen collection locations for each species. The relationship between drought frequencies across each taxon's range and life habitat (annual or perennial) was evaluated using Firth's penalized-likelihood logistic regression and phylogenetic logistic regression.

Collection dates. To test the hypothesis that annual species have adapted to escape drought prone seasons as seeds, collection dates for herbarium specimens were compared between annual and perennial species. Comparisons of distributions were made by Two-sample Kolmogorov-Smirnov test, t-test, and Barlett variance test using R (supplemental script 2) {cite R}. `### Software` We used R (Version 3.5.1; R Core Team, 2018) and the R-packages *ape* (Version 5.2; Paradis & Schliep, 2018; Orme et al., 2018;

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

Results

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* Figure 1. Using both herbarium specimen metadata and a 30 year dataset of satellite generated climate information, 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 significantly more frequent drought, and that

this signal is strongest during the summer. 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 regimes.

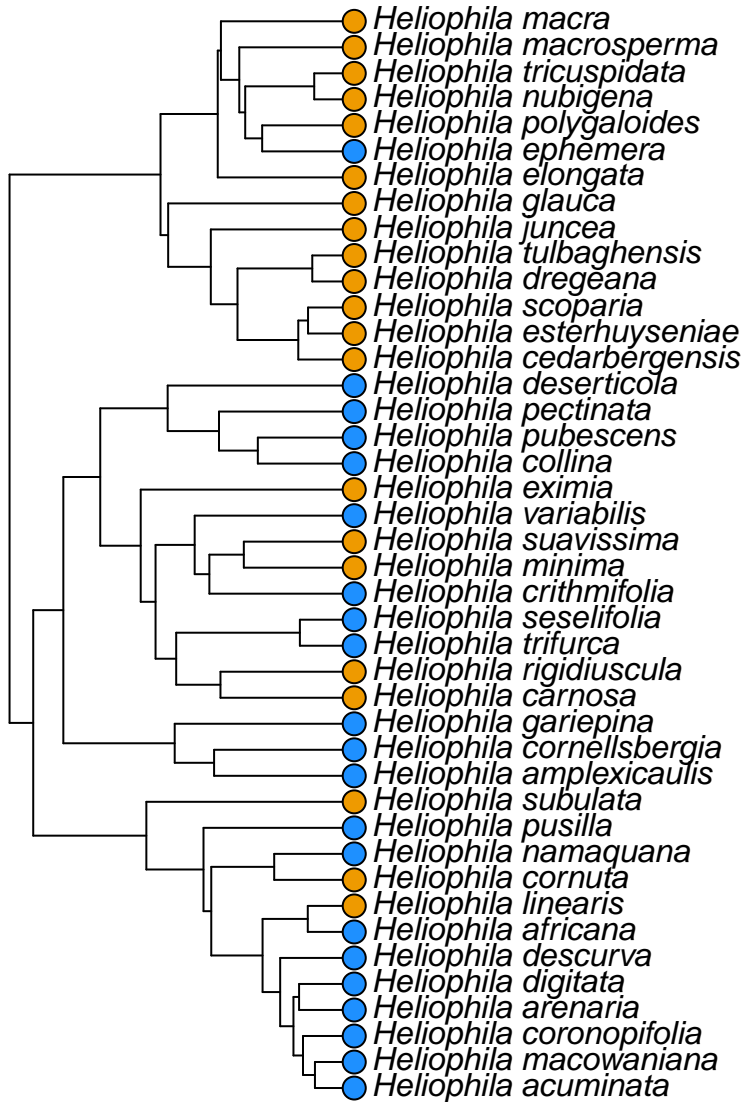


Figure 1. Phylogeny of *Heliophila*.

GBIF records. Out of 8670 *Heliophila* GBIF records, 6634 were for species with reported life history (Mummenhoff, Al-Shehbaz, Bakker, Linder, & Mühlhausen, 2005), 3653 had geospatial data, 3460 were located on pixels classified as land having drought

249 measurements, 3457 were located in Africa, 3162 were not duplicated. After all filtering
250 steps, 2192 records for 42 species (Figure ??, Table 1) passed.

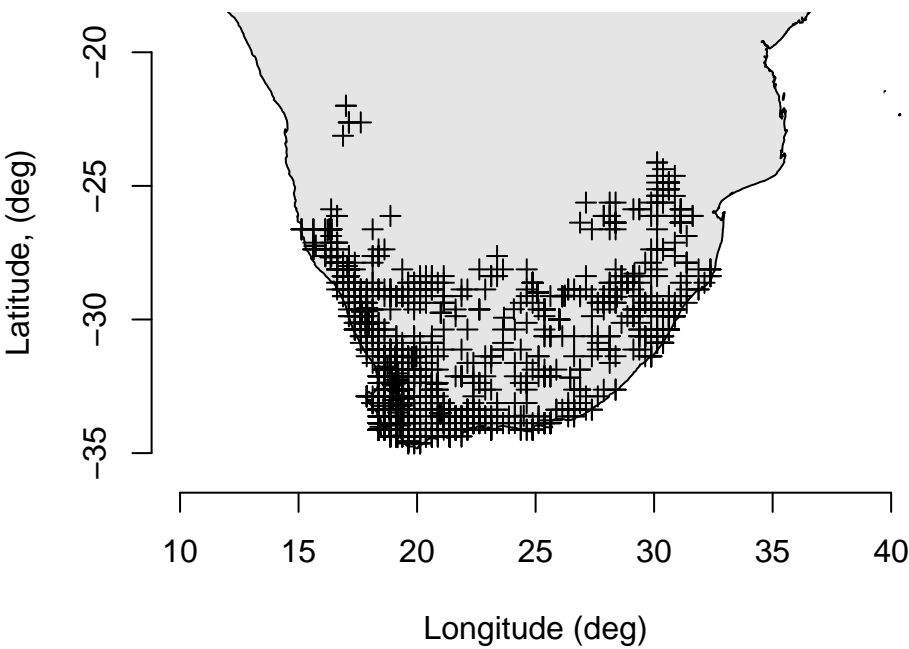


Figure 2. Map of 2192 GBIF records that passed quality filtering.

Table 1

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

Heliophila tricuspidata	p	8	0.28	0.33	0.38	0.30
Heliophila trifurca	a	77	0.45	0.48	0.48	0.43
Heliophila tulbaghensis	p	3	0.36	0.41	0.36	0.35
Heliophila variabilis	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.

Drought frequency.

Collection dates.

Discussion

Summary

We found that the distribution of annual and perennial species of *Heliophila* is significantly predicted by satellite detected historic drought frequencies. Annual species are found in environments that experience more frequent drought during the summer and fall quarters compared to perennials. This relationship was consistent while controlling for phylogenetic relatedness among the taxa studied, indicating that these distributions cannot be explained entirely by common ancestry., These results support the hypothesis that natural selection has played a role in shaping the contemporary distributions of these alternative life-history strategies.

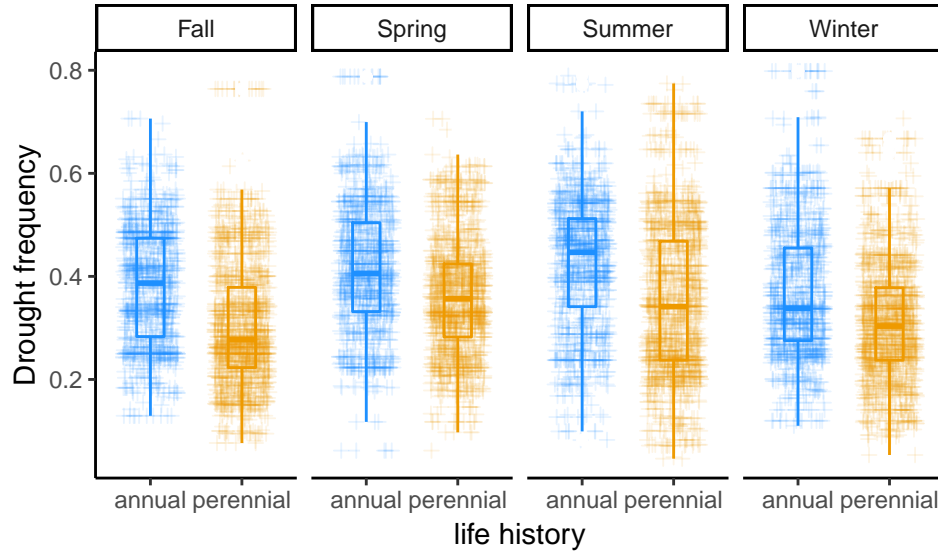


Figure 3. Comparison of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*.

Relationship to previous hypotheses/work

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

Table 2

Logistic regressions between life history, and the mean drought frequency observed at herbaria collection sites of Heliophila species.

Predictor	Estimate	p.value
Intercept	2.2575	0.1739
Winter drought freq.	-6.7484	0.1661
Intercept	4.5594	0.0443
Spring drought freq.	-11.7895	0.0423
Intercept	7.1742	0.0011
Summer drought freq.	-18.2999	0.0010
Intercept	6.4226	0.0029
Fall drought freq.	-19.0512	0.0026

Note. Firth’s penalized logistic regression.

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

Caveats

Correlation does not prove causation. But it does indicate predictive power and is consistent with adaptive hypotheses. 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, Heberling, in press). Despite these biases, the Cape Floristic region is a biodiversity hotspot and one of the most botanically well sampled

Table 3
Phylogenetically constrained logistic regressions between life history, and the mean drought frequency observed at herbaria collection sites of Heliophila species.

Predictor	Estimate	p.value
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.

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

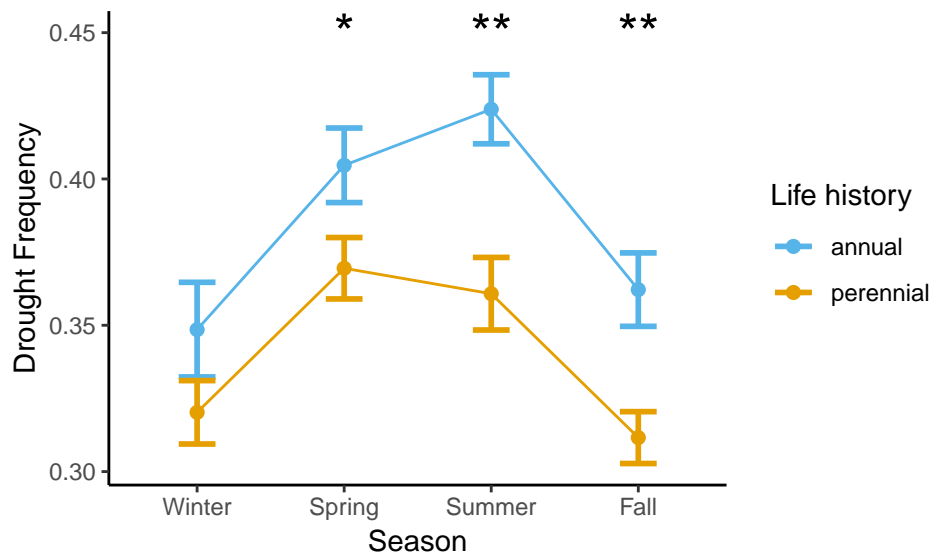


Figure 4. Comparison (mean \pm SE) of drought frequency across seasons measured at the GBIF records of annual and perennial species of *Heliophila*.

Broader implications

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

Conclusions

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

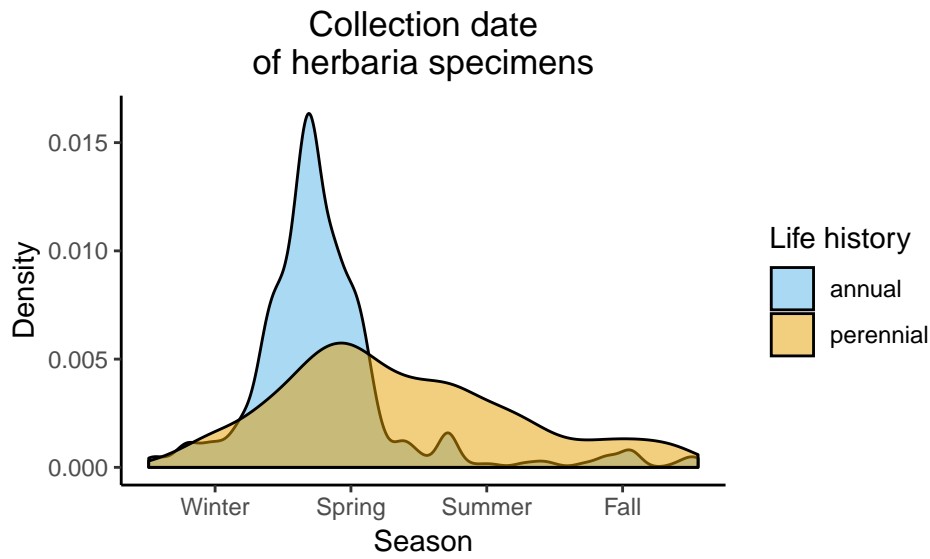


Figure 5. Collection dates of GBIF records of annual and perennial species of *Heliophila*.

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Acknowledgments

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