Drought regimens predict life history strategies in *Heliophila*

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Summary

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

• Here, we test classic life history theory in *Heliophila* L. (Brassicaceae), a diverse genus of flowering plants native to Africa, controlling for phylogeny and integrating 34 yr of satellite-based drought detection with 2192 herbaria occurrence records.

• We find that the common ancestor of these species was likely to be an annual, and that perenniality and annuality have repeatedly evolved, an estimated seven and five times, respectively. By comparing historical drought regimens, we show that annuals rather than perennial species occur in environments where droughts are significantly more frequent. We also find evidence that annual plants adapt to predictable drought regimens by escaping drought-prone seasons as seeds.

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

Introduction

Achieving an understanding of the causes of life history variation and climate adaptation is a longstanding goal of ecology and evolutionary biology (Raunkiaer, 1905; Turesson, 1925; Clausen *et al.*, 1948; Cole, 1954). In plants, life histories are especially diverse, with some species completing their life cycle in a number of weeks and others living for thousands of years (Brown, 1996). Along this continuum in angiosperms an important division exists that distinguishes annuals that complete their seed-to-seed life cycle within a single year from perennials, which can persist over multiple years. Annual plants do not need to survive through the full range of seasonal environmental variation and spend at least some portion of the year as a seed in which they are relatively protected from environmental stress. By contrast, perennial plants can continue vegetative growth over multiple years and must survive conditions experienced during all seasons, but can also benefit from competitive advantages and, if iteroparous, multiple bouts of reproduction. These represent fundamentally different life history strategies and predicting their occurrence is important for community, ecosystem and agricultural ecology. However, the environmental factors that explain their evolution and distributions remain empirically unresolved (Friedman & Rubin, 2015).

Classical theory predicts shorter life spans in environments where adult mortality is high (Charnov & Schaffer, 1973;

Stearns, 1992; Franco & Silvertown, 1996). Because lack of water is one of the greatest threats to survival during the vegetative or reproductive growth in plants, this theory has been extended to the hypothesis that annuality is adaptive when it allows plants to escape drought (Schaffer & Gadgil, 1975). Indeed, adaptation to drought, defined as episodes of increased aridity causing plant stress (Passioura, 1996), is often invoked as an explanation for the success of annual species, although drought-adapted perennials are also well known (Raunkiaer, 1905). While a few cases are cited in which annuality appears to be more common in environments with greater aridity (Stebbins Jr, 1952; Morishima *et al.*, 1984), this hypothesis has yet to be supported while controlling for the effect of common ancestry (phylogeny) on life habit. In one previous study in which this question was addressed phylogenetically, (Evans *et al.*, 2005) annuals were not found to be associated with environments that experience more drought. This could be explained by the relatively small number of species studied and the reliance on a limited number of weather stations to characterise environments, highlighting the need to develop more scalable methods to study the geographic distributions of traits such as life history. Therefore, in this study we leverage thousands of herbaria specimens among dozens of species and high-resolution remote sensing to study the distributions and environmental factors potentially driving the evolution and distribution of life history.

It is also critical to consider another dimension of drought adaptation: the expectation that annuality is most adaptive when droughts are not only frequent but also predictable. That is, when the frequency of drought is particularly high during certain seasons. Such predictability is important for selection to favour an escape strategy during seasons that are particularly drought prone. While there has been at least one example of annuality associated with environments qualitatively classified as 'predictable' in a general sense (Datson *et al.*, 2008), the seasonal predictability of drought experienced by annuals has yet to be rigorously studied. As such, further empirical work is needed to support the model of annuality as a mechanism of drought adaptation via escape from drought-prone seasons. In this paper, we examine herbarium collection dates to ask whether annuals indeed exhibit any evidence of an escape strategy from seasons with elevated drought frequency.

In addition to drought escape in annuals as a mechanism of adaptation to frequent and predictable droughts, droughts may be necessary for the success of annuals more generally by acting as episodes of disturbance that provide opportunities for annuals to establish and compete with sympatric perennial species. Indeed, there is evidence that perennials dominate in environments in which disturbance events are infrequent (Rees & Long, 1992; Corbin & D'Antonio, 2004; Clary, 2012). The resulting prediction from this hypothesis is that, in the absence of frequent drought, perenniality should evolve. However, little information is known about this component of life history evolution because previous work has focused on the origins of annuality rather than perenniality (Friedman & Rubin, 2015). This highlights the need to study taxa that have seen transitions from annual to perennial life histories as well.

In this research we combined a long-term global dataset of satellite-detected drought events with metadata from natural history collections to test these classic hypotheses within the African 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 perenniality offers competitive advantage in the absence of drought, associations between life history and drought frequency should be significant when phylogenies include 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 (that is 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 by confounding common environments caused by selection from common environments caused by ancestry. (Felsenstein, 1985; Barrett *et al.*, 1996). Therefore, we assessed the relationship between life history distribution and drought frequency while controlling for phylogeny.

Materials and Methods

Data

Data availability All analyses were performed using R. All data and the source code to produce this manuscript are available at https://github.com/greymonroe/heliophila.

Life history data for *Heliophila* *Heliophila* is a genus of flowering plants that is endemic to southern Africa including the Cape Floristic and Succulent Karoo Regions. These environments are among the most botanically diverse on Earth and the *Heliophila* species occurring there are considered to be among the most phenotypically diverse genera of the family Brassicaceae (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). This genus includes both perennial and annual species, and transitions between life history strategy may have occurred multiple independent times (Appel & Al-Shehbaz, 1997; Mummenhoff *et al.*, 2005). Furthermore, the fine scale climatic heterogeneity of southern Africa is ideal for studying the distribution of traits in relation to environmental parameters (Sayre *et al.*, 2013). We used life histories reported by Mummenhoff *et al.* (2005), grouping species into annual or perennial life history categories. Perenniality was defined as any form of perennial life history (for example herbs, shrubs, mixed). Because the nature of species reported with mixed traits were unknown (that is plasticity vs genetic variation), we classified these species here as perennial as they can maintain vegetative across multiple years at least to some capacity.

Heliophila occurrence records To characterise the distributions of annual (studied here, $n = 21$) and perennial (studied here, $n = 21$) *Heliophila* species, all (8670) records for the genus *Heliophila* were downloaded from the Global Biodiversity Information Facility (gbif.org) on 21 July 2018 (GBIF, 2018). Herbaria records such as these provide a rich data sources to characterise the geographical distributions of species (Willis *et al.*, 2017; Lang *et al.*, 2019). As they become digitised (Soltis, 2017), herbaria collections have been used to study relationships between trait distributions, geography, and climate (Davis *et al.*, 2015; Stropp *et al.*, 2016; Wolf *et al.*, 2016; Václaví'k *et al.*, 2017).

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

Satellite-detected drought data Remotely sensed data are a powerful tool for characterising seasonal patterns in drought because they are less limited in spatial and temporal scope and resolution than weather stations or field observations (AghaKouchak *et al.*, 2015). From an ecological perspective, droughts are best defined as episodes of plant stress caused by elevated aridity (Passioura, 1996). Therefore remote

sensing offers the additional benefit for studying drought as an agent of natural selection because plant stress caused by drought can be observed from space (Kogan, 1995a). The remotely sensed Vegetative Health Index (VHI) is one such metric that detects landscape scale reductions in plant and temperature conditions characteristic of drought (Kogan, 2001). Generated from data collected by NOAA AVHRR satellites since 1981, the VHI is a composite index combining Normalised Difference Vegetation Index (NDVI)-derived quantification of vegetative stress (Vegetative Condition Index – VCI) with temperature stress indicated by anomalies in thermal spectra (Temperature Condition Index – TCI). These indices were developed to create an unbiased quantification of drought across ecosystem types. The VHI of year y during week w of (1, 52) at pixel i is derived from the following equations, where n is the number of years observed:

$$\text{VCI}_{y,w,i} = 100 \frac{\text{NDVI}_{y,w,i} - \text{NDVI}_{\min,w,i}}{\text{NDVI}_{\max,w,i} - \text{NDVI}_{\min,w,i}}.$$

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

$$\text{TCI}_{y,w,i} = 100 \frac{T_{\max,w,i} - T_{y,w,i}}{T_{\max,w,i} - T_{\min,w,i}}.$$

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

$$\text{VHI}_{y,w,i} = 0.5(\text{VCI}_{y,w,i}) + 0.5(\text{TCI}_{y,w,i}).$$

By combining VCI and TCI, the VHI distinguishes drought from other forms of vegetative stress (Kogan, 1995b). The use of the VHI to detect drought has been validated globally and across ecosystem types (AghaKouchak *et al.*, 2015), including in southern Africa, the focal region of this study (for example Supporting Information Fig. S1, Monyela 2017). To date, the VHI has most often been applied for evaluating drought risk for agricultural research (for example Rojas *et al.*, 2011; Kogan *et al.*, 2016). But it also presents a tool 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 (Kerr & Ostrovsky, 2003). As such, the VHI has been applied recently to study drought-related ecology of natural species and proven useful for predicting intraspecific variation in drought tolerance traits and genes (Mojica *et al.*, 2016; Dittberner *et al.*, 2018; Monroe *et al.*, 2018b). Here, we accessed VHI data at 16 km^2 resolution from 1981 to 2015 (https://www.star.nesdis.noaa.gov/smcd/emb/vci/VH/vh_ftp.php) to characterise the seasonal drought frequencies experienced by annual and perennial *Heliophila* species across their native range of southern Africa.

Analyses

Drought frequency calculations To characterise drought regimens across the distributions of annual and perennial species of *Heliophila*, we calculated drought over different seasons at the location of observations for *Heliophila* records using the VHI. Specifically, we created maps of the frequencies of observing drought conditions between years (VHI < 40, NOAA) during the winter (quarter surrounding winter solstice), spring (quarter surrounding spring equinox), summer (quarter surrounding summer solstice) and autumn (quarter surrounding autumn equinox) from 1981 to 2015 across the range of *Heliophila*. From these maps, the drought frequency (the number of times drought is observed divided by the total number of years, 34) during the winter, spring, summer and autumn was extracted for the locations of all GBIF records.

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

- Records for species with reported life history.
- Records with geospatial data.
- Records without known geospatial coordinate issues (that is coordinates reported are those of herbarium).
- Records from collection sites classified as land pixels in the VHI dataset.
- Records from Africa (to exclude locations of cultivation).
- Records without duplicates (that is identical species, location, collection date).

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.

Phylogeny construction and ancestral state estimation Outgroup (*Aethionema grandiflorum, Alliaria petiolata, Cardamine matthioli, Chamira circaeoides,* and *Rorippa amphibia*) and in group *Heliophila* ITS I and II sequences were aligned using MAFFT (Katoh & Kuma, 2002) with strategy G-INS-I, offset value 0.1, and all other options set as default. The GTR+Γ model of nucleotide substitution was determined to best fit the data based on AIC using JMODELTEST2 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012). A maximum clade credibility tree with branch lengths as relative time was estimated by summarising data from six runs of 100 000 000 generations of Bayesian Markov chain Monte Carlo conducted in BEAST 2 (Bouckaert *et al.*, 2014). Model selection and phylogenetic analyses were conducted through the CIPRES Science Gateway (Miller *et al.*, 2010). Ancestral state estimation was performed in R using the package PHYTOOLS (Revell, 2012) to generate 10 000 stochastic character maps simulated under an equal rates model of character evolution for the trait life habit (annual or perennial). The number of transitions between annual and perennial life histories was

estimated from the average number of transitions observed in these stochastic character maps.

Comparison of drought frequency between annual and perennial species 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. We tested for a relationship between drought frequency and life history, season, and their interaction by analysis of variance while including species as a random effect using the LME4 package in R (Bates *et al.*, 2014) and compared annuals and perennials using Tukey adjusted post hoc contrasts. We next calculated the mean drought frequency during the winter, spring, summer and autumn for each species. Because shared evolutionary history of closely related species can lead to spurious associations between traits and environments (Felsenstein, 1985), we tested for a relationship between life history strategy and drought frequency while controlling for phylogeny using phylogenetic logistic regression in R with the *phylolm* package (Ives & Garland, 2010; Ho & Ane, 2014). This statistical approach is designed to control for the confounding effects of common ancestry's influence on demographic features such as geospatial relationships when addressing hypotheses about the role of natural selection on trait distributions.

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 Kolmogoro—Smirnov test and Barlett variance test in R.

Results

The topology of the estimated *Heliophila* phylogeny was consistent with previous studies (Mummenhoff *et al.*, 2005; Mandáková *et al.*, 2012). Based on 10 000 stochastic character maps simulated under an equal rates model of character evolution in life history, an average of *c.* seven changes from annual to perennial and five changes from perennial to annual were observed per stochastic character map (Fig. 1a). These results suggest that the ancestral state of *Heliophila* was annual and that both character states have arisen independently mutliple times.

After all filtering steps, 2192 records for 42 species (Fig. 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 (Figs 2, S2). While annual species were generally found in the western regions of South Africa and Namibia, primarily in the Cape Floristic Region and Succulent Karoo (Fig. 2a), the

occurrence of perennials extended to the southern and eastern coast of South Africa (Fig. 2b).

The frequency of drought varied considerably across the ranges of *Heliophila* species (Fig. 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 Namid 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, Fig. 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 autumn (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 (Fig. 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 autumn (Table 1; Fig. 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 indicated that annual species are found in environments where droughts are significantly more frequent, especially in the summer and autumn. Classic life history theory hypothesises 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 autumn 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 with perennials, which appear to be collected throughout the year, annuals are almost exclusively observed during the winter and spring (Fig. 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 seed, senesce and die before the summer. Therefore, these annual species are likely to remain dormant during the summer and autumn, when drought is the strongest predictor of the distributions of annual and perennial life histories (Fig. 3b).
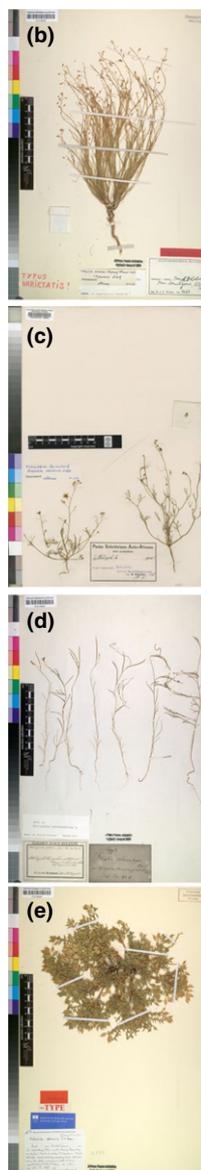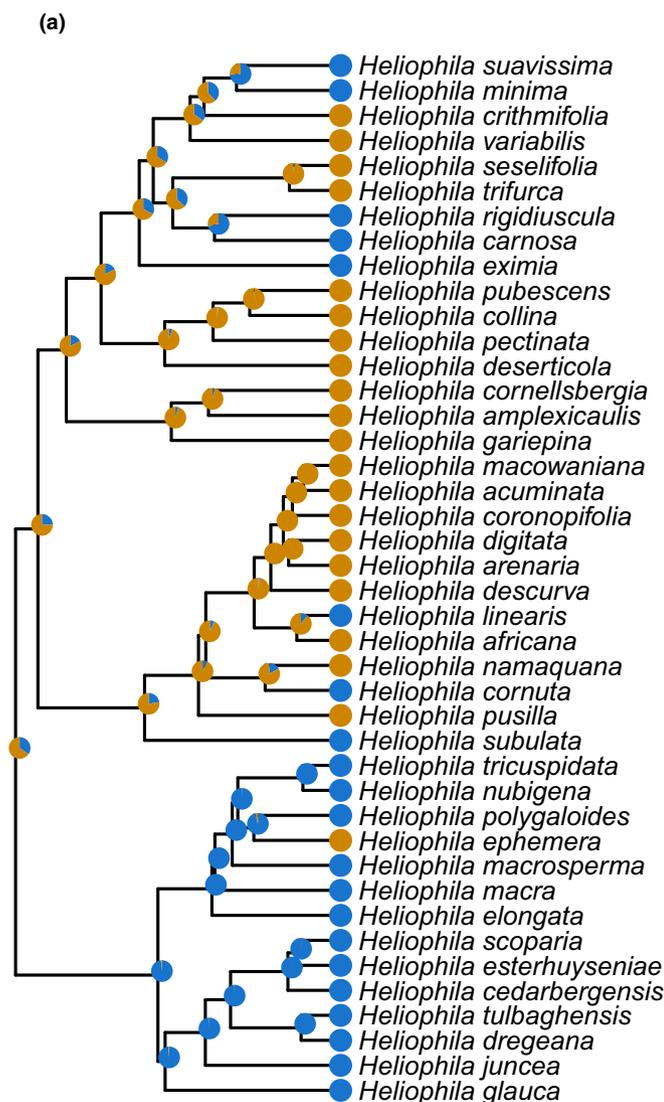
Fig. 1 Species and examples of herbaria specimens of *Heliophila* (a) Phylogeny and life history strategies of species studied. Orange circles at branch tips mark annual species and blue circles mark perennial species. At internal nodes, pie charts indicate the estimated posterior probability of being annual vs perennial. Example herbaria specimens accessed via GBIF of (b) *H. minima*, (c) *H. deserticola*, (d) *H. coronopifolia* and (e) *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 Supporting Information Notes S1.

Discussion

To test the hypothesis that annual and perennial plants reflect adaptation to alternative drought environments we examined the distributions of life history strategies in the large and diverse mustard genus, *Heliophila*. Using metadata of 2192 occurrence records and a 34-yr 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 regimes.

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

Unfortunately, herbarium collections and their associated data do not represent systematic or random sampling of a species
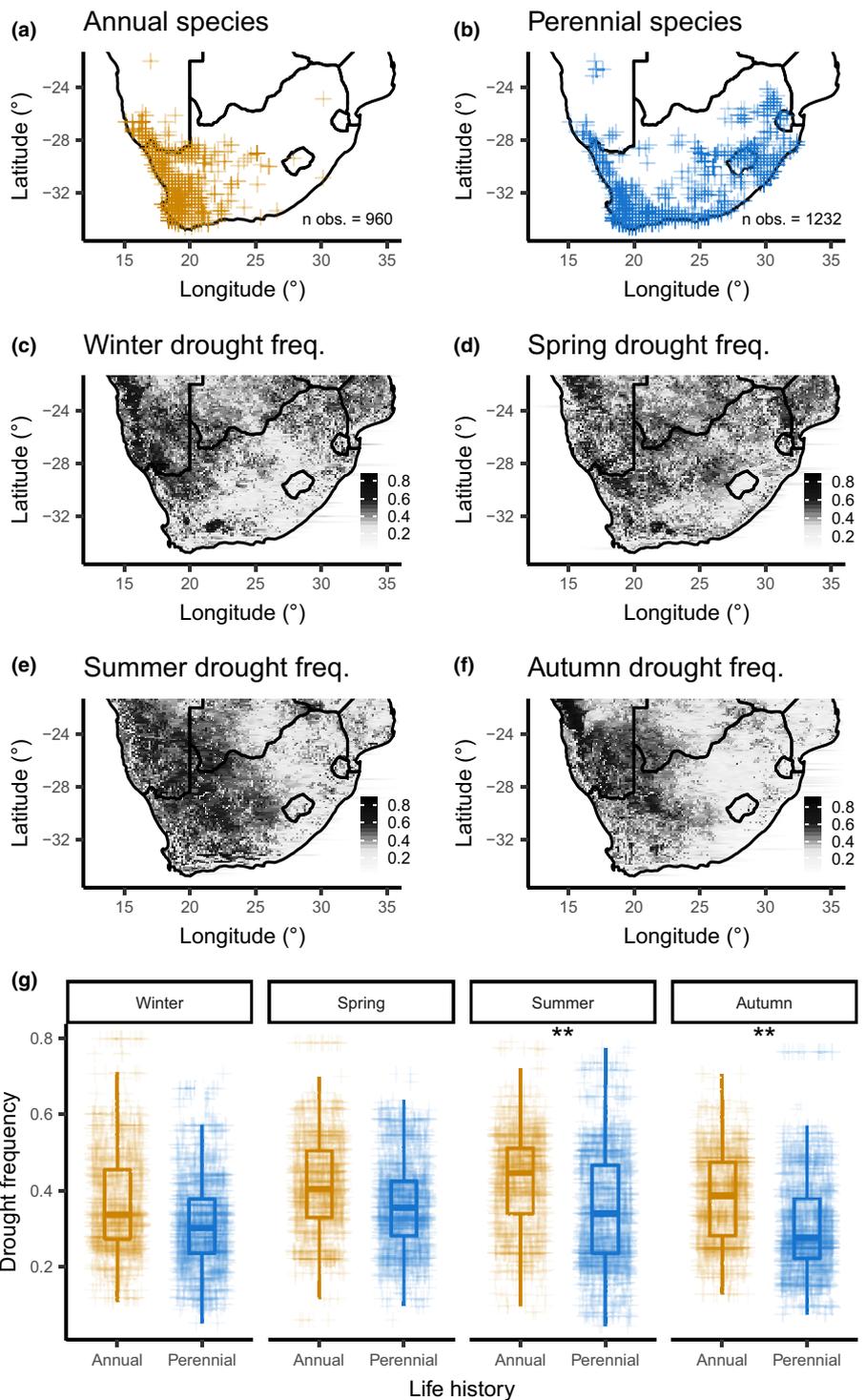
Fig. 2 Locations of occurrence records of (a) annual and (b) perennial *Heliophila*. Drought frequency during the (c) winter, (d) spring, (e) summer and (f) autumn detected using the Vegetative Health Index (VHI). (g) Drought frequencies during each season at the observation locations of annual and perennial *Heliophila* (post hoc contrasts annuals and perennials from ANOVA, **, $P < 0.01$). Boxplots indicate median (horizontal line), first and third quartiles (upper and lower limits of box), and 1.5 times the interquartile range (whiskers). Individual observations are shown by crosshairs. Annual and perennial species are indicated by data coloured blue and orange, respectively.

distribution. Significant biases in collecting exist; these have not necessarily been controlled for here, and may have some effect on our findings, such as a bias toward collecting near roads or near the locations of natural history collections (Daru *et al.*, 2018). Future research will benefit from systematic sampling efforts to avoid these noted biases. However, the ecosystems of southern Africa include several biodiversity hotspots and are among the most botanically well sampled regions on Earth (Daru *et al.*,

2018), suggesting that this may currently be the optimal region for our analyses of life history distribution. Indeed, we were able to use 2192 occurrence records to study 42 species; this represents a significant advance over relying on personal observations to characterise species distributions.

These findings empirically support classical theoretical predictions about the adaptive value of annual and perennial life history strategies. Taken together, they suggest that, in *Heliophila*,

Table 1 Phylogenetic logistic regressions between life history, and the mean drought frequency observed at specimen sites of *Heliophila* species during the winter, spring, summer and autumn.

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
Autumn drought freq.	−20.8174	0.0067

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

annual species are adapted to environments with predictable droughts by escaping drought-prone seasons during the dormant seed phase of their life cycle. They also suggest that perenniality is adaptive in environments in which droughts are less frequent. While most previous work has focused on describing the

evolutionary origins of annuality (Barrett *et al.*, 1996; Conti *et al.*, 1999; Andreasen & Baldwin, 2001; Verboom *et al.*, 2004; Friedman & Rubin, 2015) there are at least a few other cases in which perenniality appears to have arisen from an annual ancestor (Bena *et al.*, 1998; Tank & Olmstead, 2008). While early theory predicted selection for annuality when adult mortality is high (Stearns, 1992), we also found evidence that perenniality could be explained by reduced frequency of drought. This idea is supported by the theoretical prediction that perenniality is advantageous in stable habitats. Phylogeny revealed several transitions from annual to perennial life history (Fig. 1a) and the distributions of perennial *Heliophila* extended into regions where drought frequency is low (Figs 2b, S2). Perennials may be able to out compete annual relatives in environments in which the infrequency of drought favours strategies that allow plants to benefit from growth over many seasons. This also suggests that annuals rely on drought as a source of disturbance for seedling recruitment when competing with perennials (Corbin & D'Antonio, 2004). Indeed, no annual species were observed in the low drought regions of eastern South Africa (Figs 2, S2).
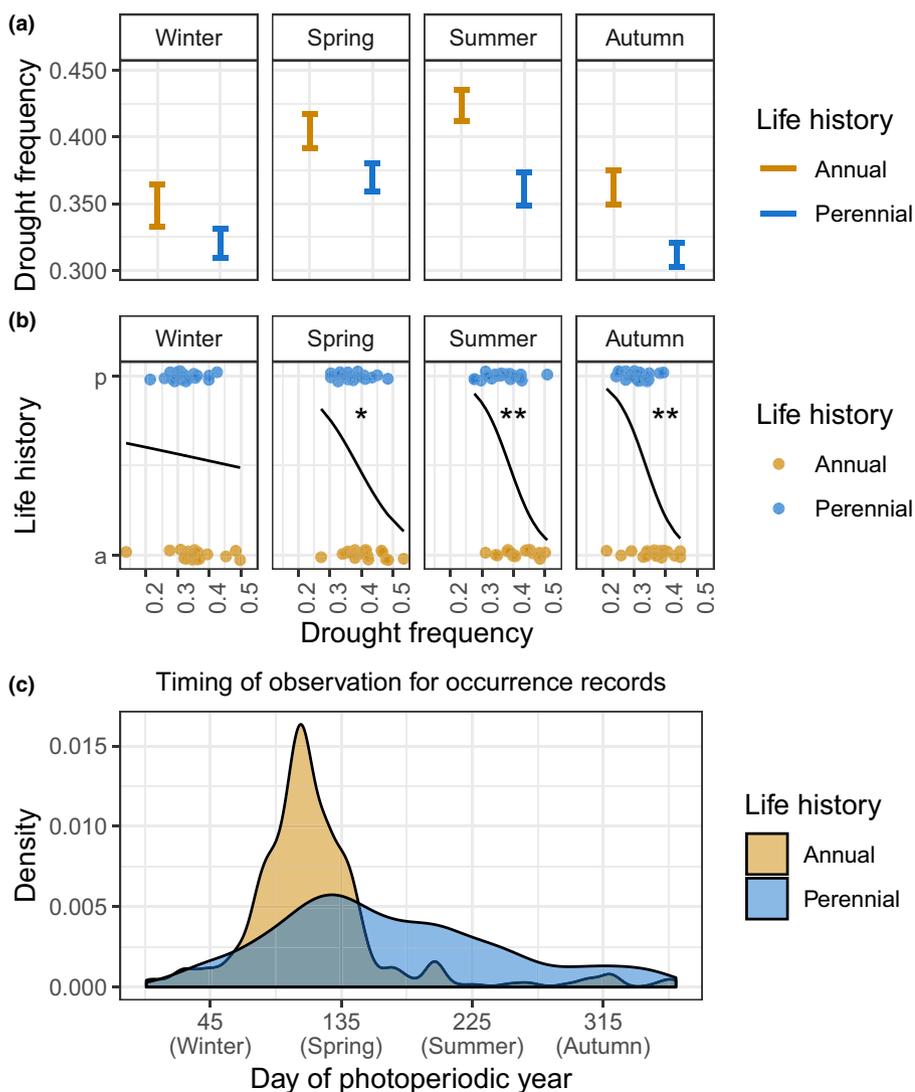

Fig. 3 Difference in drought regimens and phenology of annual and perennial *Heliophila*. (a) Comparison (mean ± SE) of drought frequency across seasons calculated at the occurrence locations of GBIF records of annual and perennial species of *Heliophila*. (b) Results from phylogenetic logistic regression, 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 autumn equinox and winter solstice.

These findings suggest that species with locally adaptive life history strategies could be threatened by rapidly changing drought regimens (Dai, 2011). In light of the findings here, forecasted reductions in rainfall across eastern South Africa (SAWS & WRC, 2017) could be particularly impactful to plant community compositions. In this analysis we found that this region is currently dominated by derived perennial species of *Heliophila*. However, a scenario in which droughts become more frequent in this region may allow for the establishment of annuals. Such changes in selection patterns and shifts in plant functional diversity could have impacts on ecosystem functioning and processes such as carbon cycling (Garnier *et al.*, 1997; Roumet *et al.*, 2006; Monroe *et al.*, 2018a). Furthermore, changes in the frequency of drought may be an important factor when considering the use of perennial cropping systems (Parry *et al.*, 2005; Lelièvre & Volaire, 2009).

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

Author contributions

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

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References

AghaKouchak A, Farahmand A, Melton F, Teixeira J, Anderson M, Wardlow BD, Hain C. 2015. Remote sensing of drought: progress, challenges and opportunities. *Reviews of Geophysics* 53: 452–480.

Andreasen K, Baldwin BG. 2001. Unequal evolutionary rates between annual and perennial lineages of checker mallows (Sidalcea, Malvaceae): evidence from 18S–26S rDNA internal and external transcribed spacers. *Molecular Biology and Evolution* 18: 936–944.

Appel O, Al-Shehbaz IA. 1997. Generic limits and taxonomy of Hornungia, Pritzelago, and Hymenolobus (Brassicaceae). *Novon* 7: 338–340.

Barrett SCH, Harder LD, Worley AC. 1996. The comparative biology of pollination and mating in flowering plants. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 351: 1271–1280.

Bates D, Mächler M, Bolker B, Walker S. 2014. Fitting linear mixed-effects models using lme4. arXiv:1406.5823.

Bena G, Lejeune B, Prosperi J-M, Olivieri I. 1998. Molecular phylogenetic approach for studying life-history evolution: the ambiguous example of the genus *Medicago* L. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265: 1141–1151.

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard M, Rambaut A, Drummond A. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 10: e1003537.

Brown PM. 1996. OLDLIST: a database of maximum tree ages. *Tree Rings, Environment, and Humanity. Radiocarbon* 1996: 727–731.

Charnov EL, Schaffer WM. 1973. Life-history consequences of natural selection: Cole's result revisited. *American Naturalist* 107: 791–793.

Clary J. 2012. Determinants of perennial and annual grass distribution in Mediterranean-climate California. *Plant Ecology* 213: 1203–1208.

Clausen J, Keck DD, Hiesey WM. 1948. *Experimental studies on the nature of species. III. Environmental responses of climatic races of Achillea.* Washington, DC, USA: Carnegie Institution, iii–129.

Cole LC. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29: 103–137.

Conti E, Soltis DE, Hardig TM, Schneider J. 1999. Phylogenetic relationships of the silver saxifrages (*Saxifraga*, sect. Ligulatae Haworth): implications for the evolution of substrate specificity, life histories, and biogeography. *Molecular Phylogenetics and Evolution* 13: 536–555.

Corbin JD, D'Antonio CM. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* 85: 1273–1283.

Cruz-Mazo G, Buide M, Samuel R, Narbona E. 2009. Molecular phylogeny of Scorzoneroides (Asteraceae): evolution of heterocarpy and annual habit in unpredictable environments. *Molecular Phylogenetics and Evolution* 53: 835–847.

Dai A. 2011. Drought under global warming: a review. *Wiley Interdisciplinary Reviews: Climate Change* 2: 45–65.

Darriba D, Taboada G, Doallo R, Posada D. 2012. JModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.

Daru BH, Park DS, Primack RB, Willis CG, Barrington DS, Whitfeld TJ, Seidler TG, Sweeney PW, Foster DR, Ellison AM et al. 2018. Widespread sampling biases in herbaria revealed from large-scale digitization. *New Phytologist* 217: 939–955.

Datson P, Murray B, Steiner K. 2008. Climate and the evolution of annual/perennial life-histories in *Nemesia* (Scrophulariaceae). *Plant Systematics and Evolution* 270: 39–57.

Davis CC, Willis CG, Connolly B, Kelly C, Ellison AM. 2015. Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American Journal of Botany* 102: 1599–1609.

Dittberner H, Korte A, Mettler-Altmann T, Weber AP, Monroe G, de Meaux J. 2018. Natural variation in stomata size contributes to the local adaptation of water-use efficiency in *Arabidopsis thaliana*. *Molecular Ecology* 27: 4052–4065.

Evans ME, Hearn DJ, Hahn WJ, Spangle JM, Venable DL. 2005. Climate and life-history evolution in evening primroses (Oenothera, Onagraceae): a phylogenetic comparative analysis. *Evolution* 59: 1914–1927.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.

Franco M, Silvertown J. 1996. Life history variation in plants: an exploration of the fast-slow continuum hypothesis. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 351: 1341–1348.

Friedman J, Rubin MJ. 2015. All in good time: understanding annual and perennial strategies in plants. *American Journal of Botany* 102: 497–499.

Garnier E, Cordonnier P, Guillerm J-L, Sonié L. 1997. Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. *Oecologia* 111: 490–498.

GBIF. 2018. GBIF occurrence download. [WWW document] URL https://doi.org/10.15468/dl.xmwqxm [accessed 21 July 2018].

Guindon S, Gascuel O. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology* 52: 696–704.

Ho LST, Ane C. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology* 63: 397–408.

Ives A, Garland T. 2010. Phylogenetic logistic regression for binary dependent variables. *Systematic Biology* 59: 9–26.

Katoh M, Kuma M. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066.

Kerr JT, Ostrovsky M. 2003. From space to species: ecological applications for remote sensing. *Trends in Ecology & Evolution* 18: 299–305.

Kogan FN. 1995a. Droughts of the late 1980s in the United States as derived from NOAA polar-orbiting satellite data. *Bulletin of the American Meteorological Society* 76: 655–668.

Kogan FN. 1995b. Application of vegetation index and brightness temperature for drought detection. *Advances in Space Research* 15: 91–100.

Kogan FN. 2001. Operational space technology for global vegetation assessment. *Bulletin of the American Meteorological Society* 82: 1949–1964.

Kogan F, Guo W, Strashnaia A, Kleshenko A, Chub O, Virchenko O. 2016. Modelling and prediction of crop losses from NOAA polar-orbiting operational satellites. *Geomatics, Natural Hazards and Risk* 7: 886–900.

Lang PL, Willems FM, Scheepens J, Burbano HA, Bossdorf O. 2019. Using herbaria to study global environmental change. *New Phytologist* 221: 110–122.

Lelièvre F, Volaire F. 2009. Current and potential development of perennial grasses in rainfed Mediterranean farming systems. *Crop Science* 49: 2371–2378.

Mandáková T, Mummenhoff K, Al-Shehbaz IA, Mucina L, Mühlhausen A, Lysak MA. 2012. Whole-genome triplication and species radiation in the southern African tribe Heliophileae (Brassicaceae). *Taxon* 61: 989–1000.

Mojica JP, Mullen J, Lovell JT, Monroe JG, Paul JR, Oakley CG, McKay JK. 2016. Genetics of water use physiology in locally adapted Arabidopsis thaliana. *Plant Science* 251: 12–22.

Miller M, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop*: 1–8.

Monroe J, Markman D, Beck W, Felton A, Vahsen M, Pressler Y. 2018a. Ecoevolutionary dynamics of carbon cycling in the anthropocene. *Trends in Ecology & Evolution* 33: 213–225.

Monroe J, Powell T, Price N, Mullen J, Howard A, Evans K, Lovell J, McKay J. 2018b. Drought adaptation in *Arabidopsis thaliana* by extensive genetic loss-of-function. *eLife* 7: e41038.

Monyela BM. 2017. A two-year long drought in summer 2014/2015 and 2015/2016 over South Africa. PhD thesis, University of Cape Town, Cape Town, South Africa.

Morishima H, Sano Y, Oka H. 1984. Differentiation of perennial and annual types due to habitat conditions in the wild rice *Oryza perennis*. *Plant Systematics and Evolution* 144: 119–135.

Mummenhoff K, Al-Shehbaz IA, Bakker FT, Linder HP, Mühlhausen A. 2005. Phylogeny, morphological evolution, and speciation of endemic Brassicaceae genera in the Cape flora of southern Africa. *Annals of the Missouri Botanical Garden* 92: 400–424.

Parry M, Flexas J, Medrano H. 2005. Prospects for crop production under drought: research priorities and future directions. *Annals of Applied Biology* 147: 211–226.

Passioura J. 1996. Drought and drought tolerance. *Plant Growth Regulation* 20: 79–83.

Raunkiaer CC. 1905. Types biologiques pour la géographie botanique. *Oversigt over Det Kongelige Danske Videnskabernes Selskabs Forhandlinger* 347–438.

Rees M, Long MJ. 1992. Germination biology and the ecology of annual plants. *American Naturalist* 139: 484–508.

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

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

Roumet C, Urcelay C, Dı́az S. 2006. Suites of root traits differ between annual and perennial species growing in the field. *New Phytologist* 170: 357–368.

SAWS & WRC. 2017. *A climate change reference atlas*. Pretoria, South Africa: The South African Weather Service.

Sayre RG, Comer P, Hak J, Josse C, Bow J, Warner H, Larwanou M, Kelbessa E, Bekele T, Kehl H *et al.* 2013. *A new map of standardized terrestrial ecosystems of Africa*. African Geographical Review. Washington, DC, USA: Association of American Geographers.

Schaffer W, Gadgil M. 1975. Selection for optimal life histories in plants. In: Cody M, Diamond J, eds. *The ecology and evolution of communities*. Cambridge, MA, USA: Belknap, 142–157.

Soltis PS. 2017. Digitization of herbaria enables novel research. *American Journal of Botany* 104: 1281–1284.

Stearns SC. 1992. *The evolution of life histories*. Oxford, UK: Oxford University Press.

Stebbins GL Jr. 1952. Aridity as a stimulus to plant evolution. *American Naturalist* 86: 33–44.

Stropp J, Ladle RJ, Malhado ACM, Hortal J, Gaffuri J, Temperley WH, Olav Skøien J, Mayaux P. 2016. Mapping ignorance: 300 years of collecting flowering plants in Africa. *Global Ecology and Biogeography* 25: 1085–1096.

Tank DC, Olmstead RG. 2008. From annuals to perennials: phylogeny of subtribe Castillejinae (Orobanchaceae). *American Journal of Botany* 95: 608–625.

Turesson G. 1925. The plant species in relation to habitat and climate: contributions to the knowledge of genecological units. *Hereditas* 6: 147–236.

Václavı́k 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 remote sensing data. *PLoS ONE* 12: e0175671.

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: Ehrhartoideae). *American Journal of Botany* 91: 1364–1370.

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: phenological research using herbarium specimens. *Trends in Ecology & Evolution* 32: 531–546.

Wolf A, Zimmerman NB, Anderegg WR, Busby PE, Christensen J. 2016. Altitudinal shifts of the native and introduced flora of California in the context of 20th-century warming. *Global Ecology and Biogeography* 25: 418–429.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Example years experiencing contrasting degrees of drought in southern Africa.

Fig. S2 Maps of occurrence records for individual *Heliophila* species.

Notes S1 Sources for images of herbarium specimens in Fig. 1.

Table S1 *Heliophila* species records and the mean drought frequencies during different seasons at the location 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.

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