

Shifts in the abiotic and biotic environment of cultivated sunflower under future climate change[☆]

Zia Mehrabi^{1,*}, Samuel Pironon^{2,*}, Michael Kantar³, Navin Ramankutty¹ and Loren Rieseberg⁴

¹ UBC School of Public Policy and Global Affairs and Institute for Resources, Environment, and Sustainability, University of British Columbia, Vancouver, BC V6T 2K9, Canada

² Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK

³ Department of Tropical Plant and Soil Sciences, University of Hawai'i, Mānoa, 3190 Maile Way, Honolulu, HI 96822, USA

⁴ Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

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Abstract – Sunflower is a unique model species for assessing crop responses and adaptation to climate change. We provide an initial assessment of how climate change may influence the abiotic and biotic environment of cultivated sunflower across the world. We find an 8% shift between current and future climate space in cultivated sunflower locations globally, and a 48% shift in Northern America, where the crop originates. Globally, the current niche occupied by sunflower crop wild relatives offer few opportunities to adapt to future climate for cultivated sunflower, but in Northern America 100% of the future climate space of cultivated sunflower is filled by the niche of primary wild relative germplasm alone (*e.g.* wild *Helianthus annuus*). Globally, we find little difference in the overlap between current and future climate space of cultivated sunflower with the niche of the important sunflower pathogen *Sclerotinia sclerotiorum*, but in Northern America, climate change will decrease the overlap between local populations of this pest and cultivated sunflower by 38%. Our analysis highlights the utility of multi-scale analysis for identifying candidate taxa for breeding efforts and for understanding how future climate will shift the abiotic and biotic environment of cultivated crops.

Keywords: sunflower / crop wild relatives / climate niche / pest pressure / global / Northern America

Résumé – Changements dans l'environnement biotique et abiotique du tournesol cultivé, dans le contexte du changement climatique futur. Le tournesol est une espèce modèle unique pour évaluer les réactions des cultures et leur adaptation au changement climatique. Nous fournissons une première évaluation de la manière dont le changement climatique peut influencer l'environnement abiotique et biotique du tournesol cultivé à travers le monde. Nous constatons un décalage de 8% entre l'espace climatique actuel, et futur dans les sites de culture de tournesol à l'échelle mondiale et de 48% en Amérique du Nord, d'où la culture est originaire. Au niveau mondial, la niche actuelle occupée par les plantes sauvages apparentées aux cultures de tournesol offre peu de possibilités d'adaptation au climat futur pour le tournesol cultivé, mais en Amérique du Nord, 100% de l'espace climatique futur est occupé uniquement par la niche de matériel génétique primaire (par exemple, *Helianthus annuus* sauvage). Globalement, le chevauchement entre l'espace climatique actuel, et futur du tournesol cultivé et la niche de l'agent pathogène important du tournesol, *Sclerotinia sclerotiorum*, varie peu. En Amérique du Nord, le changement climatique réduira de 38% le chevauchement entre les populations locales de ce ravageur et le tournesol cultivé. Notre analyse souligne l'importance de l'analyse multi-échelle pour identifier les taxons candidats aux efforts de sélection et pour comprendre, comment le climat futur modifiera l'environnement abiotique et biotique des cultures.

Mots clés : tournesol / cultures sauvages parents / niche climatique / pression des ravageurs / global / Amérique du Nord

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* Correspondence: zia.mehrabi@ubc.ca

^a These authors contributed equally to the manuscript

1 Introduction

Sunflower is a unique model species for assessing crop responses and adaptation to climate change (Badouin *et al.*, 2017). It is widely cultivated and has close relatives that can be found growing in many saline, heat stressed, and drought stricken conditions (Kantar *et al.*, 2015; Mason & Donovan 2015; Seiler *et al.*, 2017). It also carries many nutritional benefits, is high in protein (20% by seed dry weight); antioxidants such as Vitamin E (only 40 g providing daily requirements); and essential polyunsaturated fats (up to 60–70% linoleic content for common, non High-Oleic types) (USDA, 2017). To date there has been extensive work to characterise the phenotypes and genetics of sunflower crop wild relatives in their native range (Seiler 2007; Kane & Rieseberg 2007; Mandel *et al.*, 2011; Kalyar *et al.*, 2014; Kantar *et al.*, 2015; Mason & Donovan 2015; Seiler *et al.*, 2017); which, combined with the recent sequencing of the sunflower genome (Badouin *et al.*, 2017), opens up new opportunities for expedited breeding of cultivars that are both adapted to extreme conditions and carry nutritional benefits.

Yet despite this promise, and accumulating knowledge that climate change may impact sunflower in Europe (e.g. Debaeke *et al.*, 2017), little is still known about how the abiotic and biotic stressors of cultivated sunflower may change under future climate, and the degree to which crop wild relatives may help adapt to these shifts globally. Filling this knowledge gap is an essential first step to better understand climate adaptation for sunflower itself, and to determine how well research on sunflower may be applied to breeding climate resilient varieties in other major food crops.

In this paper, we provide an initial assessment of how future climate change may influence the abiotic and biotic environment of cultivated sunflower across the world – identifying if future climate will present new conditions under which sunflower farmers may need to adapt. We, then, assess the degree to which the climate niche of sunflower crop wild relatives overlap with predicted future shifts in the climate of cultivated sunflower – identifying if current climate experienced by crop wild relatives offer insights into breeding climatic tolerance from the wild sunflower gene pool. Finally we assess, whether, shifts in climate in sunflower growing locations are conducive or hostile to the climatic niche of *Sclerotinia sclerotiorum*, to identify if biotic stress is likely to increase or decrease in future, and what opportunities there may be for breeding abiotic tolerances that also help escape pest pressure. We chose *Sclerotinia sclerotiorum* because it is a widespread pest causing yield losses (Dorrell & Huang 1978; Gulya *et al.*, 1989), for which cultivated sunflower holds only weak resistance. We undertake our analysis across two scales – at the global level, and in Northern America within the native range of sunflower wild relatives – allowing us to assess the benefits of wild relatives for adaptation, *versus* current management practices in the cultivated range of sunflower. Finally, we situate our results in the context of ongoing sunflower research, and more generally in efforts for breeding climate resilient crops worldwide.

2 Methods

2.1 Occurrence data

We drew on three primary geospatial data sets for this analysis. For the current distribution of cultivated sunflower, we used Monfreda *et al.* (2008), which represents harmonized census data of cultivated sunflower, centered on the year 2005 and 2000, and downscaled to 5×5 arc minutes ($0.083 \times 0.083^\circ$) pixels by fusion with cropland area in a land cover product classified from MODIS satellite imagery (Ramankutty *et al.*, 2008). To be conservative, and to minimise erroneous observations for low resolution census data in minor sunflower producing countries, we disregarded pixels with $<10\%$ fractional cropland coverage at the 5 arc minute resolution, and converted the remaining pixels into presences, and absences. We then upscaled these Boolean data into 10 arc minutes ($0.167 \times 0.167^\circ$), by considering any presence within the finer resolution as evidence of occurrence. For the distribution of crop wild relatives, we draw on the data presented in Kantar *et al.* 2015, which represent 4705 records of 36 crop wild relatives taxa in the primary, secondary and tertiary gene-pool (Harlan & de Wet, 1971), geo-located in their native range in Northern America. For the distribution of *Sclerotinia sclerotiorum*, we extracted occurrences from CABI's PlantWise database on May 21st 2018 (<https://www.plantwise.org/>). As this data is of varying precision (*i.e.* some are derived from national level distribution maps and expert opinion, others from primary records), we only used data with at least 10 arc minutes spatial resolution.

2.2 Climate data

To characterize the climate ranges of the different species, we extracted current and future climatic information from version 1.4. of the Worldclim database (Hijmans *et al.*, 2005). We collected eight different bioclimatic variables at a 10 arc minutes resolution ($0.167 \times 0.167^\circ$) that represent mean, seasonal, and extreme temperature and precipitation conditions: annual mean temperature (BIO1), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual mean precipitation (BIO12), precipitation of the wettest (BIO13) and driest (BIO14) months, and precipitation seasonality (BIO15). For future conditions, we used 20-year average climate data (already at 10 arc minutes) representing the 2070 time period (averages for 2061–2080) generated by 15 downscaled global climate models (ACCESS 1-0 (AC), BCC-CSM1-1 (BC), CCSM4 (CC), CNRM-CM5 (CN), HadGEM2-AO (HD), HadGEM2-CC (HG), HadGEM2-ES (HE), INMCM4 (IN), IPSL-CM5A-LR (IP), MIROC-ESM-CHEM (MI), MIROC-ESM (MR), MIROC5 (MC), MPI-ESM-LR (MP), MRI-CGCM3 (MG), and Nor-ESM1-M (NO)), and two greenhouse gas emission scenarios (Representative Concentration Pathways (RCP) 4.5 and 8.5) used in the fifth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2014). We extracted current and 2070 climate data at each species occurrence point using the *raster* package (Hijmans, 2016) in R (R Core Team, 2017).

2.3 Climate niche analyses

We defined the current climate niche for cultivated sunflower, for each of the 36 crop wild relatives, for *Sclerotinia sclerotiorum*, and the future climatic space expected for cultivated sunflower using a simple two-step convex hull approach. First, we undertook principle component analysis (PCA) of the eight bioclimatic variables at each of the presence locations, to extract axes representing the majority of variation in climatic space for occurrences. We used the *ade4* package (Dray *et al.*, 2017) to perform the PCAs. Second, we fit a convex hull to the principle component axes 1 and 2 to identify the boundaries of the climatic niches for each plant and pest species, using base R and the *sp* package (Pebesma & Bivand, 2017). Because the intensity of sampling of occurrence records can be uneven in both geographic and climatic spaces, it cannot be considered a good proxy for species abundance—which is particularly important for the occurrence records of crop wild relatives and pests. For this reason, we used convex hulls that do not rely on point density, contrary to other commonly used techniques (Blonder, 2017). However, convex polygons are highly sensitive to sparse occurrences of location records at the edge of the climatic space. Given that some occurrences at the margins of climate space could be due to sampling errors, we reconstructed the convex hulls using six increasing distance thresholds (Mahalanobis distance) between the occurrence records and the centre of the species climate space to obtain a range of estimates of climatic niches.

To estimate the expected future change in climatic conditions, where sunflower is currently cultivated, we measured the overlap between its current and future climate spaces as the percentage of the total area of the convex hull representing future conditions covered by the polygon representing the current climate niche. This measure was repeated 180 times, for the 180 different scenarios (15 GCMs, 2 RCPs, and 6 convex hull selections methods). To obtain one single robust overlap value, we computed the median across these 180 different combinations.

We assume that the future climatic space not occupied by the crop represents a potential need for climate adaptation. We assessed whether wild relatives were currently occupying these new future climatic conditions by estimating the percentage of the future climate polygon that overlaps with the current climate niches of each wild relative species and of all of the wild relatives aggregated together. Again, robust estimates were obtained by computing the median overlap values computed across the 180 different GCM/RCP/convex hull selection combinations. We repeated this analysis for *Sclerotinia sclerotiorum* in order to evaluate how biotic and abiotic stresses might interact to affect sunflower cultivation in the future. All analyses were conducted at both global and Northern America (United States and Canada) scales. A full set of reproducible code for the niche analysis methods used in this paper is forthcoming (S. Pironon and colleagues).

2.4 Annotated cladogram

To visualize the evolutionary relationships between the different crop wild relatives and to map their climate niche overlap with future climate space of cultivated sunflower, we

constructed a cladogram of the hypothesized relationships using Stephens *et al.* (2015) backbone updated with Baute *et al.* (2016). The remaining taxa, not present in these two analyses, were placed on the cladogram using the phylogeny presented in Kantar *et al.* (2015). Some crop wild relatives may be misidentified by taxonomists, but we were unable to correct for these across all the taxa in our study, and so present the results based on the original accession data. Where in depth genomic analysis challenges species identities (*e.g.* *H. petiolaris/H. neglectus*, *H. bolanderi/H. exilis*, *H. winteri/H. annuus*) (Baute *et al.*, 2016), we maintain separate nodes for accession species identities and simply label them as sister taxa.

In addition to annotating this cladogram with the climate niche overlap values, we added annotations of two traits indices which relate to climate gradients and disease resistance, where data were available. The first index we used is the “Leaf Economics Spectrum” (or “LES”), a principle component axis reported to explain ~52% of the variance in 6 leaf traits (*e.g.* leaf lifespan, leaf mass per area, rates of photosynthesis and night time respiration, and concentrations of nitrogen and phosphorus) for certain wild relatives in our analyses set. Higher LES axis values for these taxa indicate more resource acquisitive species (with higher relative growth rates) found in fertile, cool and dry environments, and lower values indicate more resource conservative species (with slower growth rates), found in soil nutrient poor, hot and wetter environments (Mason & Donovan, 2015). The second trait index, we used, is a disease resistance index representing mean resistances to leaf blight (*Alternaria helianthi*), head rot (*Rhizopus spp.*), and powdery mildew (*Erysiphe chicoracearum*) compiled from the literature (Mason *et al.*, 2016). To compute the disease index, resistance assay scores were first normalized to lie between 0 and 1 by dividing by the maximum resistance score within the species set for that assay, and then scores were averaged within and then across disease types, to produce a single index. Notably, not all species in our study had trait data available, and resistance data was not complete or consistent across species (see Mason & Donovan, 2015; Mason *et al.*, 2016 for details). Resistance assays specific to *Sclerotinia sclerotiorum* was not available for inclusion, and this composite index is only used as a proxy for general disease resistance in crop wild relatives as used in our analysis. Graphical display was done in R with the *ggplot2* and *ggtree* packages (Yu & Lam, 2018; Wickham *et al.*, 2018).

3 Results

We find that, based on our current knowledge of where sunflower is cultivated globally, the climate niche of cultivated sunflower overlaps strongly with the climate it will likely experience in the future. There is only a small, ~8%, shift in the current and future climate space in cultivated locations globally (Fig. 1). This story changes dramatically when the analysis is focussed on Northern America—with a 48% shift in the current and future climate space in cultivated locations (Fig. 1C). These differences in scale of analysis impact directly on the apparent opportunities for adaptation presented by crop wild relatives. Indeed, on the global level we find that crop wild relatives across all gene pools (primary, secondary, and tertiary) which are native to Northern America would seemingly offer limited opportunity

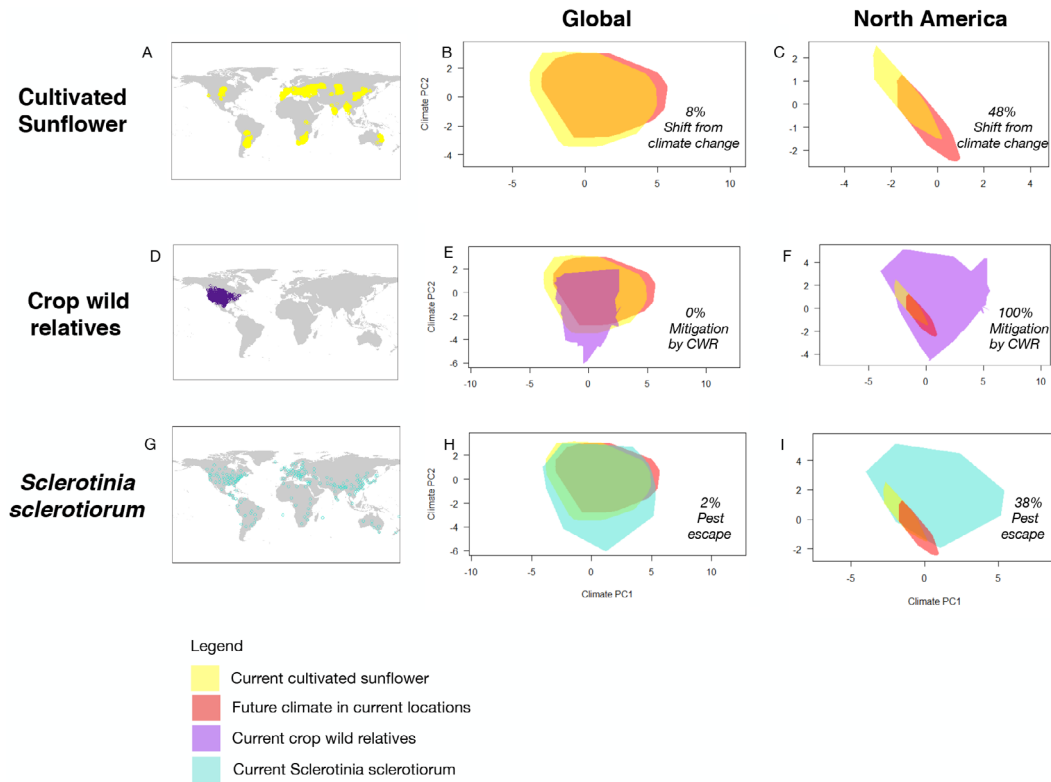


Fig. 1. Shifts in cultivated sunflower climatic space with climate change expected by 2070. A. Current global distribution of cultivated sunflower. B. Shift in climate space in cultivated locations globally. C. Shift in climate space in cultivated locations in N. America. D. Global distribution of sunflower crop wild relatives (CWR). E. Potential for CWRs to adapt to future climate conditions globally. F. Potential for CWRs to adapt to future climate conditions in N. America. G. Global distribution of major sunflower pest (*Sclerotinia sclerotiorum*). H. Escape of *Sclerotinia sclerotiorum* under future climate globally. I. Escape of *Sclerotinia sclerotiorum* under future climate in Northern America. Numbers and graphi graphical representations represent the median result from 15 GCMs, 2 RCPs and 6 occurrence selection thresholds. Figures represent the unlikely worst-case scenario (*i.e.* high emissions, low mitigation), RCP 8.5, with the CCSM4 GCM, to illustrate maximum losses of climate space. CWRs = crop wild relatives.

for mitigating the future climate that will be experienced by current sunflower growing locations across the world (Fig. 1E). However, when analyzed on the scale of Northern America, the benefits of crop wild relatives are much more apparent – with mitigation potential of 100% of the future growing conditions that cultivated sunflower will experience outside its current climate niche (Fig. 1F). All (*i.e.* 100%) of future climate space in Northern America could be filled within the primary germplasm alone (*e.g.* wild *Helianthus annuus*) – which was the best performing crop wild relatives species by far (Fig. 2). Interestingly, relationships between the niche overlap of wild relatives and the future climate of cultivated sunflower, resource economics traits, and disease resistance traits, all appeared largely idiosyncratic, suggesting no obvious trade-offs between these traits (Fig. 2).

Globally and in Northern America we find a large overlap between the climatic niche of the pest *Sclerotinia sclerotiorum* and cultivated sunflower (Figs. 1H–1I). This suggests that even if *Sclerotinia sclerotiorum* is not found in all current sunflower growing locations, there is high potential for spread and proliferation of this pest, even under current climates. At a global level, due to the minimal difference between current and future climate space in cultivated sunflower locations, we find minimal potential for sunflower to escape *Sclerotinia sclerotiorum*; with

only ~2% of future climate space in growing locations sitting outside the climate niche of this pest (Fig. 1H). When we run the analysis on the scale of Northern America the story is again different. The future climate in currently cultivated sunflower locations offers a potential opportunity to escape *Sclerotinia sclerotiorum* with ~38% of the future climate falling outside the current niche of this pest within the Northern American range (Fig. 1).

4 Discussion

Breeding climate resilient crops with the use of crop wild relatives has been proposed as a major strategy to adapt to future climate change (Dempewolf *et al.*, 2014; Graham 2017). Our analysis, which is equivalent to a climate analog approach (Pugh *et al.*, 2016; CGIAR, 2018), sheds some interesting perspectives on shifts in the abiotic and biotic environment for cultivated sunflower under future climate, and identifies the scope of opportunities for breeding for future climates using knowledge of where wild germ plasm are locally adapted today.

We find that domesticated sunflower is cultivated across wide temperature and precipitation gradients that on a global

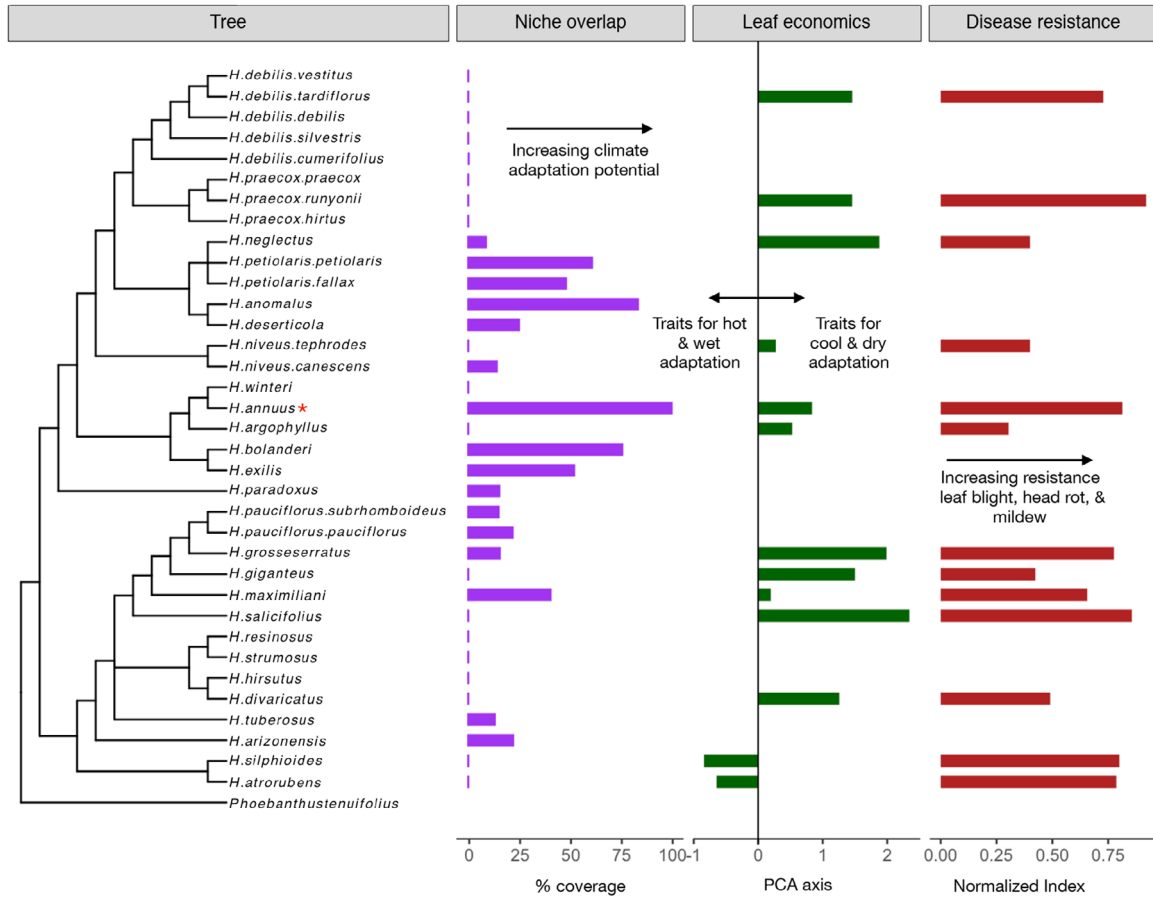


Fig. 2. Annotated cladogram showing the overlap in climatic niche of sunflower crop wild relatives and future climate space of cultivated sunflower in Northern America. Median percent niche overlap values are shown in purple. Leaf economics trait data which explain physiological syndromes differences between species, and geographically correlate with environmental variables such as average temperature and precipitation are shown in green, and an index of fungal disease resistance for each CWR are shown in red (See in Fig. 1 and methods for more details). Gaps in the plots indicate no data.

level seem to outstrip the narrow realized climate niche space of sunflower crop wild relatives in their native range in Northern America. We think this is unlikely to be idiosyncratic to sunflower or dependent solely on data quality of what we currently know about where sunflower is grown. Crops often thrive outside their centres of origin and crop wild diversity (Khoury *et al.*, 2016). Humans have expanded the niche for crops, for example by eliminating competition and adding nutrients and water; however, current cultivated areas of sunflower are also likely narrower than its fundamental niche because of competition from other crops for growing areas. This does not necessarily mean that wild relatives will not be useful for climate adaptation, but that our current knowledge of where wild relatives grow may have limited potential for identifying climate adaptation opportunities. For insight into the utility of crop wild relatives, we likely need to rely on ecophysiological studies and common garden comparisons.

Indeed, numerous studies indicate that crop wild relatives appear to have increased resistance to abiotic and biotic stress than domesticated varieties (Luedders & Dickerson 1977; Smedegaard-Petersen & Tolstrup, 1985; All *et al.*, 1989; Mayrose *et al.*, 2011; Koziol *et al.*, 2012). The problem here

lies in whether it is feasible to introgress these traits into domesticated lines without loss of yield or other desirable qualities. Domestication and improvement have enhanced resource acquisitive traits (*e.g.* large thin leaves), which increase yields but in turn may increase susceptibility to abiotic stress or pathogen attack (Mariotte *et al.*, 2018). Indeed, in sunflower, greater stem thickness and flowering head size have increased susceptibility to *Sclerotinia* – giving the impetus to breed resistance (Burke & Rieseberg, 2003). However, the data for the species and pathogens, we were able to obtain data for suggests there is no clear trade-off between resource acquisition and general disease resistance. Moreover, for abiotic resistance, biogeographic analysis of these crop wild relatives challenge the idea of a clear trade-off between drought tolerance and resource acquisition (Mason & Donovan, 2015). Plastic changes in root architecture can also occur without a significant yield penalty to relative growth (Bowsler *et al.*, 2016), and inducible resistance to diseases can reduce fitness costs of resistance because the response is only activated upon exposure to stress (Karasov *et al.*, 2017). These findings, along with other phenotypic and genetic studies (Chapin *et al.*, 1993; Reich *et al.*, 2003; Bailey-Serres *et al.*,

2012; Turner *et al.*, 2014), suggest that the commonly held view of trade-offs between stress tolerance and yield may need revisiting.

For many crops, increased pathogen spread under climate change remains an important concern (Bebber *et al.*, 2014). In Northern America, we show that the future climate space in current cultivated sunflower locations may allow it to escape the pest *Sclerotinia sclerotiorum* given its current known distribution in the continent. However, for Northern American farmers to benefit, not only must cultivated varieties be able to persist in new climate space and the pest be locally maladapted, but strong phytosanitary mechanisms would be required to ensure global pest populations already adapted to the future climate space of sunflower in Northern America do not spread. Due to the large overlap in climate niches of *Sclerotinia sclerotiorum* and cultivated sunflower globally, we worry that climate endowed pest escape may have limited prospects. In Northern America in 2016, the gross production value of sunflower seed was \$485.6 million USD (\$462.4 US, \$23.2 Canada) (FAO, 2015). Under free dispersal of this pest, and blanket yield losses of 4–37% (Dorrell & Huang 1978; Gulya *et al.*, 1989), we might expect elasticity unadjusted risk to farm gate from *Sclerotinia sclerotiorum* to be between \$19.4–\$197.6 million dollars per year for Northern America. While future work using mechanistic models would be required to better understand the spread of this pathogen further, the lack of strong resistance to this pest in cultivated sunflower (Vear & Grezes-Besset, 2010), and broad climate niche of this pest globally, suggests tackling resistance is likely to remain a priority, even where periods of climate enabled pest escape appear possible.

One question that arises from an analysis such as ours is: could farmers in Northern America learn from other locations globally, if climate in these other locations matches the majority of future climate space for this crop in Northern America? We think this is an important question, and believe that the value added from breeding efforts should be weighed against this possibility. One reason why this might not work is that in Northern America cultivation might be limited by different factors, such as more co-evolved pests and pathogens, rather than management practices, such as irrigation, which may remove limits to cultivation elsewhere. Another consideration is that future population growth and demands on natural systems will likely increase pressures on other resources, such as water and energy for irrigation, which may limit the transferability of apparently successful management across borders and into the future. We suggest that the impact of climate change and opportunities for breeding climate resilient crops be assessed in the backdrop of these wider resource challenges and constraints, and alongside the costs of education, knowledge and skills transfer of successful cultivation in analog climates across the world.

In closing, our assessment of shifts in climate in current growing areas of cultivated sunflower helps to shed some light on how abiotic and biotic stressors of this crop might change under future climate change. Climate analog models can be useful but as we have discussed carry some limitations too. A sharpened linking of cultivated sunflower and crop wild relatives adaptation potential may need to come from defining geographically explicit climate production functions for cultivated sunflower and identifying physiological proxies

that relate strongly to yield responses that can be assayed in both cultivated plants and wild types under common climate conditions. For sunflower—looking at management in its broader distribution of cultivation outside its native range in Northern America, and identification of tolerance traits that will work with domesticated syndromes seem essential.

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