

**EXPLORING THE RESILIENCE AND OPTIMIZING THE USES OF  
POTATO WILD RELATIVE SPECIES (*SOLANUM* SECTION *PETOTA*)  
IN A CHANGING CLIMATE**

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## **Chapter 1: Interactions between breeding system and ploidy affect niche breadth in Solanum**

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## **Abstract**

Understanding the factors driving ecological and evolutionary interactions of economically important plant species is important for sustainability. Niches of crop wild relatives, including wild potatoes (*Solanum* section *Petota*), have received attention, however, such information has not been analyzed in combination with phylogenetic histories, genomic composition, and reproductive systems. We used a combination of ordinary least-squares (OLS) and phylogenetic generalized least-squares (PGLM) analyses to identify the discrete climate classes that wild potato species inhabit in the context of breeding system and ploidy. Self-incompatible diploid or self-compatible polyploid species significantly increase the number of discrete climate niches inhabited. This result was sustained when correcting for phylogenetic non-independence in the linear model. Our results support the idea that specific breeding system and ploidy combinations increase niche divergence through the decoupling of geographical range and niche diversity, and therefore, these species may be of particular interest for crop adaptation to a changing climate.

## Introduction

Potato (*Solanum tuberosum* L.) is the most important tuber crop worldwide and is the fourth most important crop internationally (Castañeda-Álvarez et al. 2015). However, there is a lack of genetic diversity among many crops, including *S. tuberosum* (Jansky et al., 2013; Khoury et al., 2014), placing increased pressure upon crop management protocols and food security. A proven approach to increasing genetic diversity in crop species is through the utilization of wild relatives for crop improvement (Jansky et al., 2013; Mehrabi et al., 2019). Cultivated potato has 199 known wild relatives, forming the *Solanum* section *Petota*, inhabiting 16 countries in the Americas, and ranging from 38° N to 41° S (Hijmans, 2001); 72 of the most threatened and useful species to humans have recently been prioritized for conservation (Castañeda-Álvarez et al., 2015). These 72 species are most found in tropical highlands at 600 to 1200 m in elevation and possess phenotypes similar to cultivated potato through the production of a starchy tuber (Hijmans, 2002).

Given the importance of maintaining the crop's productivity, many attributes of the wild relatives of *S. tuberosum* have been defined, including their ploidy, breeding system, germplasm classification, endosperm balance number, single and multi-gene phylogenies, and geographic ranges (Hijmans, 2001; Spooner, 2001; Spooner, 2007; Castañeda-Álvarez et al., 2015; Robertson et al., 2011). These data can be used to discover novel beneficial characteristics present within the wild relative germplasm such as biotic and abiotic resistances as well as to quantify trait introgression. Furthermore, research has identified potato as one of the crops in Sub-Saharan Africa with the highest potential to benefit from crop wild relatives for climate change adaptation, however, these results have not been integrated with biological (e.g., breeding system and ploidy) and evolutionary (e.g., phylogenetic tree) information (Pironon et al., 2019). Despite the wide array of information surrounding the wild relatives of potato, one attribute continues to be under-defined - the discrete

climate zones (e.g., niche) each species inhabits, and the factors involved (e.g., breeding system, ploidy) in driving the evolution of the highly dynamic climatic diversity in *Solanum* section *Petota*.

Individually exploring life history traits (Wendel and Cronn, 2003; Hijmans et al., 2007; Köhler et al., 2010; Sessa, 2019) such as the breeding system has led to contradictory conclusions regarding these traits' influence on ecological niche (Peterson et al., 1999; Husband et al., 2008; Robertson et al., 2010; Campbell, 2013; Grossenbacher et al., 2016; Park et al., 2017; Grant, 2020), while exploring other traits such as ploidy (te Beest et al., 2012; Van De Peer et al., 2017; Baniaga et al., 2020) has shown a consistent influence. For example, diversification models Zenil-Ferguson et al. (2019) showed that ploidy is the most probable pathway to evolve self-compatibility across Solanaceae. Therefore, there exists an important interaction between ploidy and breeding system (Barringer, 2007; Husband et al., 2008; Robertson et al., 2010) that might impact evolutionary and ecological processes (Sessa, 2019). Furthermore, polyploidization facilitates self-compatibility because whole genome duplication provides security against inbreeding depression (Barringer, 2007; Husband et al., 2008; Robertson et al., 2010; Zenil-Ferguson et al., 2019); whereas self-compatible diploid populations often suffer from large inbreeding depression (Barringer and Geber, 2008; Husband and Schemske, 2017). As a result, diploid populations are more reliant on self-incompatibility to drive adaptive changes. In *Solanaceae*, polyploid species show higher rates of self-compatibility (Barringer, 2007; Husband et al., 2008; Robertson et al., 2010). This clear interaction between ploidy and breeding systems provides the opportunity to test two key hypotheses: first, that self-compatible species rely on polyploidy in order to generate the variation they need to colonize diverse niche space; and second, that diploid species rely on outcrossing to increase niche breadth through gene flow.

To identify the driving factors of ecological diversity in potato wild relatives, we investigated two biological aspects of ecological diversity - breeding system and ploidy in 72 wild relatives of potato. We combined species' occurrence, climatic, biological (e.g., breeding system and ploidy), and phylogenetic tree of *Solanum* taxa to test whether the niche diversity of a given species is guided by a specific breeding system and ploidy interaction. To account for the potential decoupling of geographical range and niche breadth (Randel et al., 2009), the measure of climatic diversity is through the use of discrete climate-classification of each occurrence of these wild relative species. This work supports classic ecological theory of niche divergence without the requirement of inferring continuous species distributions from point-based climate descriptions by featuring the relationship between two common intrinsic factors of niche expansion: (1) decreased reliance on outcrossing reproduction of polyploid variants; and (2) increased reliance on outcrossing reproduction of diploid variants (Roughgarden, 1972; Barton, 1996; De Bodt et al., 2005; Johnson et al., 2014).

## Materials and Methods

### *Data Collection*

Data organization and analyses were conducted using the R (R Core Team, 2020) packages “raster” (Hijmans, 2020) and “tidyverse” (Wickham et al., 2019). We obtained 49,165 occurrence records of the 72 *Solanum* species sourced from Castañeda-Álvarez et al (2015). These occurrences represent the most threatened and useful wild relatives of *Solanum tuberosum*, the previously cleaned points were further filtered for those lacking latitudinal and/or longitudinal information, resulting in a total of 37,032 total occurrence points (Castañeda-Álvarez et al., 2015). Next, the Köppen-Geiger three-tier climate class system was acquired from Rubel and Kottek (2010). The Köppen-Geiger climate class system divides climates into five main groups that are subdivided based on seasonal precipitation and temperature that result in 30 potential discrete classes globally (reviewed in Rubel and Kottek, 2010). The Köppen-Geiger is one of the most widely used systems for analyzing ecological conditions and identifying primary types of plants of a latitudinal and longitudinal intersection. Three-tier climate classes were extracted at each occurrence point. The total number of climate classes per species was counted for each species and climate classes with three or fewer occurrences were removed in order to avoid “by-chance” occurrences. Using discrete climate classes allows for a single measure of both niche diversity and breadth. See github repository “[https://github.com/Nfumia/Potato\\_nichediversity\\_drivers](https://github.com/Nfumia/Potato_nichediversity_drivers)” for code and data files.

### *Linear Models for Climate Classes*

A linear model was fitted using R package “stats” (R Core Team, 2020) to identify which interaction of biological factors is correlated with niche diversity in *Solanum* section *Petota*. We used the number of discrete climate classes in which each taxon can occur as a proxy for niche breadth, as these niches vary spatially within the five broad descriptors of tropical, dry, temperate, continental, and

polar each of which possessing 2-12 subclassifications. For example, *S. stoloniferum* has fifteen discrete niches in which it occurs, but *S. albornozii* has only one, a temperate oceanic environment. The number of discrete climate classes is the response variable for the model. The predictor variables were combinations of ploidy (Castañeda-Álvarez et al., 2015) and breeding system (Robertson et al., 2010; Zenil-Ferguson et al., 2019) for each species, which were coded as dummy variable interaction terms: self-incompatible diploid, self-compatible diploid, self-compatible asexually propagating polyploid, and unknown breeding system asexually propagating diploid.

#### *Phylogenetic Tree and Phylogenetic Linear Models*

A Bayesian molecular clock phylogeny with time-calibration of section *Petota* to outgroups of domesticated tomato (*Solanum lycopersicum*) and domesticated eggplant (*Solanum melongena*) was estimated using 32 plastid genomes and compared to the most recent time-calibrated phylogeny of Särkinen et al. (2013). Due to a lack of plastid genome availability for some species in *Solanum* section *Petota*, only 27 of the 72 prioritized wild relative species were present in our subsequent analyses. Furthermore, 32 species (27 potato wild relatives, 2 domesticated potato, 1 domesticated tomato, 1 tomato wild relative, 1 domesticated eggplant) were aligned using the software MAFFT (multiple alignment using fast Fourier transform) via maxiterate version (Katoh, 2009). MrBayes (Huelsenbeck and Ronquist, 2001) as implemented in the Geneious software package (Kearse et al., 2012) was used to conduct an initial phylogenetic analysis (Vallejo-Marín and O'Brien, 2006; Newton et al., 1999). We used a chain length of 10 million generations with 25% (or 2.5 million) burn in and a subsampling frequency every 1,000 generations. The General Time Reversible (GTR) substitution model was employed for the Bayesian analysis with rate variation of gamma, including 4 categories.

We used the Bayesian uncorrelated relaxed clock-model dating method as implemented in BEAST2 (Bouckaert et al., 2019). The uncorrelated relaxed clock-model allows for rate variation across branches and measures for rate autocorrelation between lineages. Node ages are estimated simultaneously in BEAST2, and, therefore, uncertainty is incorporated into the node-age estimation. Our Bayesian MCMC tree output was used as a starting phylogeny. The Hasegawa-Kishino-Yano (HKY) model for DNA base pair substitution was used to better estimate the substitution rates of transition versus transversion as well as the Felsenstein (F81) proposed four-parameter model. A Kappa of 2.0, as estimated by BEAUti2 (Bouckaert et al., 2019), was employed. Calibration points for the node-age estimation were sampled from Särkinen et al. (2013) to create calibration priors: (1) tomato – potato split circa 8 mya (95% HPD 7—10), and (2) eggplant – tomato/potato split circa 14.3 mya (95% HPD 13-16). These calibration points reflect a normal distribution with standard deviations of 0.85 and 1.10 million years, respectively. Yule tree prior with uniform distribution was used given all ingroup and outgroup species in this study currently persist *ex-situ* and/or *in-situ*. Priors were manually generated for each monophyletic clade showing greater than 85% posterior probability from the MrBayes MCMC analysis. Default priors were used for all other parameters. A total of 100 million generations, 10 runs with 10 million generations each, were run in BEAST2 (Bouckaert et al., 2019).

Using the time-calibrated phylogeny (Figure 1), we estimated the phylogenetic generalized linear models' version of the OLS models proposed in the previous section to account for potential phylogenetic signals in the errors (Felsenstein, 1985; Hansen, 1997). This is an important step, since it is possible that our explanatory variables are not tracking the evolutionary history of the *Petota* section and can incorrectly conclude strong correlations between the climatic classes and the life history traits (Uyeda et al., 2018).

These phylogenetic linear models were estimated using a maximum likelihood PGLM with the R package “phylolm” (Ho and Ane, 2014). For all the PGLMs we assumed a Brownian motion model of evolution (Grafen, 1989; Martins and Hansen, 1997; Revell and Harmon, 2008). Outgroup species and cultivated potato were removed at this point due to the inability to differentiate between cultivated and wild occurrence of the given species. This resulted in retention of 27 potato wild relative species, comprising the four major monophyletic clades of section *Petota* (Spooner et al., 2014), for use in the PGLMs analysis.



## Results

### *Climate Regression*

The 72 prioritized species in the *Solanum* section *Petota* examined here occurred in 17 distinct climates with individual species distributions ranging from a single climate (e.g., *S. albornozi*, *S. chilliasense*, *S. lesteri*) to 15 distinct climates (e.g., *S. stoloniferum*). Within this range exists a spectrum of breeding system and ploidy combinations between and within these species and their populations, exhibiting different extents of climate niche diversity (Figure 2). This analysis showed that distinct breeding system and ploidy combinations existed in a different number of niches ( $p = 3.4 \times 10^{-7}$ ), described as the number of discrete Köppen-Geiger climate classes. Species that possess populations that are self-incompatible diploid and self-compatible polyploid show the greatest mean climate diversity with 11 discrete climate classes (Figure 2). Self-incompatible diploid species exhibit a greater average niche diversity when compared to self-compatible diploid species (Figure 2). Furthermore, diploid species possessing populations showing polyploidization demonstrate greater sustained ecological divergence.

The maximum likelihood intercept value of ecological niche diversity is  $2.81 \pm 1.01$  climate classes. Species existing as self-incompatible diploid or self-compatible polyploid have significantly ( $p$ -value  $< 0.01$ ) larger climatic niches by  $3.13 \pm 0.73$  and  $3.62 \pm 0.79$  discrete climate classes, respectively (Table 1). However, other predictor (self-compatible diploid, asexually propagating unknown breeding system diploid) variable slope values are not significantly different from zero, and, therefore, they exert no measurable influence on niche diversity within *Solanum* section *Petota*. Overall, the model explained a moderate amount of variance with an adjusted R-square of 0.39.

### *Evolutionary Climate Regression*

In the PGLMs fitted using our estimated time-calibrated phylogeny (Figure 3), we found an estimated intercept value of  $6.43 \pm 1.67$  (Table 2). The PGLMs confirmed the correlations of OLS models, with self-incompatible diploid ( $3.98 \pm 1.04$ ) and self-compatible polyploid ( $2.57 \pm 0.98$ ) significantly increasing ecological diversity (Table 2). As with OLS, the other predictor variables in PGLMs are not significantly different from zero.

## Discussion

Clarifying the impacts of plant traits on niche divergence is important to understanding the structure of global patterns of biodiversity and evolution in plant lineages (Cavender-Bares et al., 2009).

Furthermore, life history traits can provide clues about the potential resiliency of plants with increased development of wild areas leading to changes in habitat and climate for many species.

However, resilience may be tightly linked with other characteristics. In *Solanum* section *Petota*, the interaction of two specific characters, breeding system and ploidy, explain a large portion of the variation in niche divergence. The models presented here, OLS and PGLMs, explain 39% and 44% (R-squared), respectively, of the climatic niche variation present within *Solanum* section *Petota* with two alternate ends of the biological spectrum serving as the most significant predictors. On one end, self-incompatible diploid species exhibit the greatest significant correlation to climatic niche diversity within potato wild relatives. Such sustained diversity is likely the result of constant capacity for outcrossing between these species and their subsequent heterogenous design, fashioning an adaptive and resilient population through long-distance gene flow (Loveless and Hamrick, 1984). Due to the interaction between ploidy and breeding system, self-incompatible diploid species show niche diversity similar to self-compatible polyploid species, confirming the dynamic nature of the *Solanaceae* system (Barringer, 2007; Husband et al., 2008; Robertson et al., 2010; Zenil-Ferguson et al., 2019). However, self-fertilizing polyploid species have a short-term advantage as they can colonize new environments with very few individuals.

For all the *Solanaceae* family self-incompatible diploid has been shown to be the ancestral state (Zenil-Ferguson et al., 2019), they also have faster net diversification compared to all self-compatibles, both diploid and polyploid (Wright et al., 2013). The expectation given the success of these lineages in diversification is that self-incompatible diploids should have broader niches, an

unexpected result was that self-compatible polyploids diversified in a similar way. Evolutionarily this may be a temporal effect, polyploids are successful in short time scales and this may explain the success in diversification identified here, however, this study does not disentangle evolutionary timescales. Our results suggest that self-compatible diploids appear evolutionarily transient, and the evolution of self-compatibility appears to occur very rarely without a polyploidy event in Solanaceae. This suggests that polyploidy is just an evolutionary byproduct of trying to become self-compatible, allowing for rapid establishment in many new environments.

Self-compatible polyploid species have increased climatic niche diversity which, given their increased genetic variation and plasticity through additional sets of chromosomes, make them capable of adaptive and resilient population generation (Soltis and Soltis, 1999). Polyploidy allows self-fertilizing section *Petota* species to maintain and derive novel diversity typically observed in outcrossing/self-incompatible diploid populations. These differences between breeding system and ploidy with niche diversity provide support for the use of these variable combinations as driving evolutionary forces, with qualitative results (Figure 2) being supported by OLS (Table 1) and PGLMs (Table 2).

Our results suggest the potential to use ecologically plastic species to enhance the adaptability of cultivated potato lines in the face of climate change. The ultimate goal of this investigation is increased beneficial genetic variation among cultivated potato varieties developed through introgression of the various wild adaptations. However, the wild species have limited cross-compatibility with *S. tuberosum*, as evidenced in their endosperm balance numbers. Therefore, time is needed in order to operationalize this diversity in agricultural fields, so that favorable environmental adaptations from a subset of ecologically plastic species, can be introgressed while breaking linkages to agronomically unfavorable traits.

The impact of breeding system on the evolution of climatic niche diversity amongst plants is still unclear and the *Solanum* section *Petota* system contributes important evidence for a multilayered role where breeding system and ploidy interact synergistically with one another. In one case, self-incompatible breeding systems play a large role in sustaining niche diversity over time (Park et al., 2017) when species are diploid, possessing limited reproductive barriers. In contrast, self-compatible breeding systems comparatively increase niche diversity when species are polyploid, by enhancing their ability to reach, reproduce, establish, and adapt (Campbell, 2013) with the biological safety net of increased “buffering capacity” through genetic variation (Wendel and Cronn, 2003). Further investigations could focus on the decoupling of breeding system and ploidy; however, due to the self-incompatibility conferred by S-RNases found in polyploid populations of *Solanaceae* this is challenging (Robertson, 2010; Barringer, 2007; Husband et al., 2008). Furthermore, this study was not able to completely decouple ploidy and breeding system interactions due to lack of data on particular species’ breeding systems, exemplifying the need for more than DNA collection. Additionally, a limitation of this analysis is the limited number of species available for PGLMs, which was due to a lack of publicly available plastid genome sequence data.

Increasing effective genetic diversity through polyploidization has the potential to increase the number of niches to a similar extent as would occur with an outcrossing diploid population. The breeding system is the main driver of niche divergence in the self-incompatible diploid populations, while only a secondary contributor in the self-compatible polyploid populations. Despite the biological differences, the resulting niche diversity is not seen in a difference of preferred climate type but rather the extent of climatic diversity (Figure 4). Through decoupling geographical range size and niche breadth (Randel et al., 2009), this study tests classic theory by utilizing a highly diverse, economically important section of plants. Our findings lend credence to the hypothesis that these ecologically plastic responses evolved over millions of years in species with populations of self-

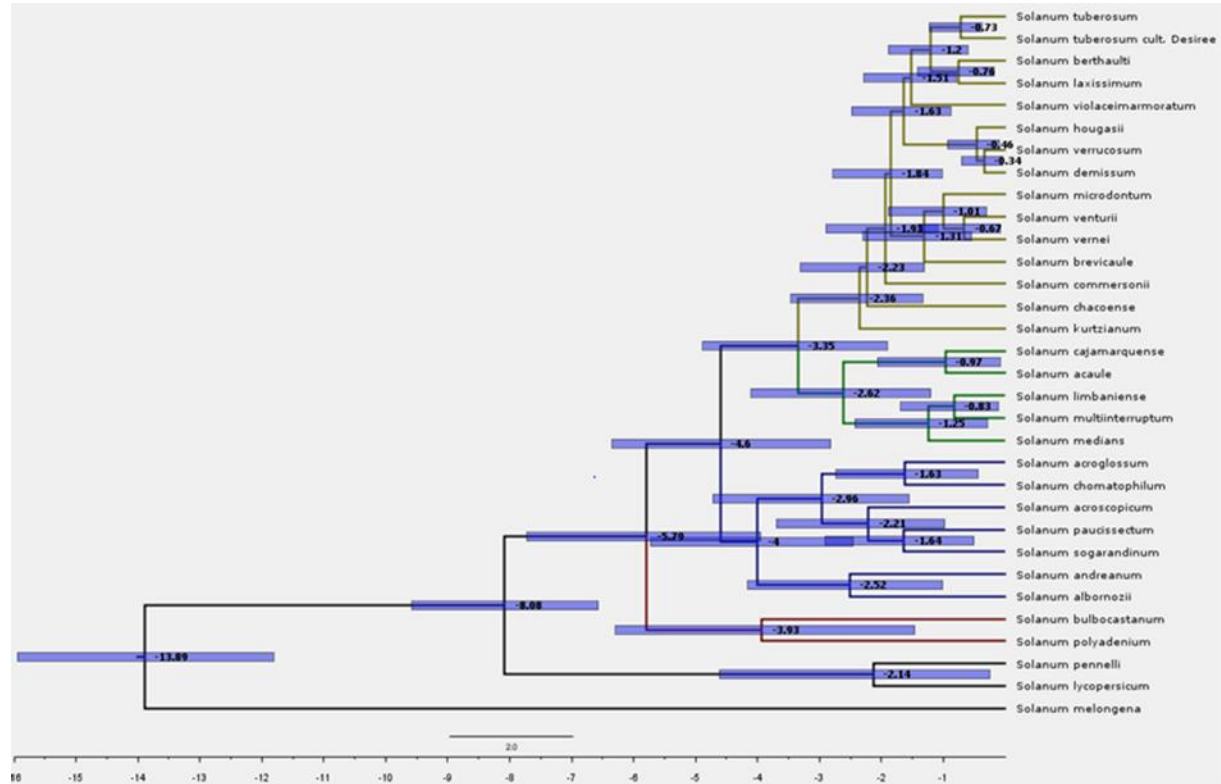
incompatible diploids and self-compatible polyploids, and, therefore, these species should be prioritized for conservation and for use to adapt our cultivated varieties to a changing climate.

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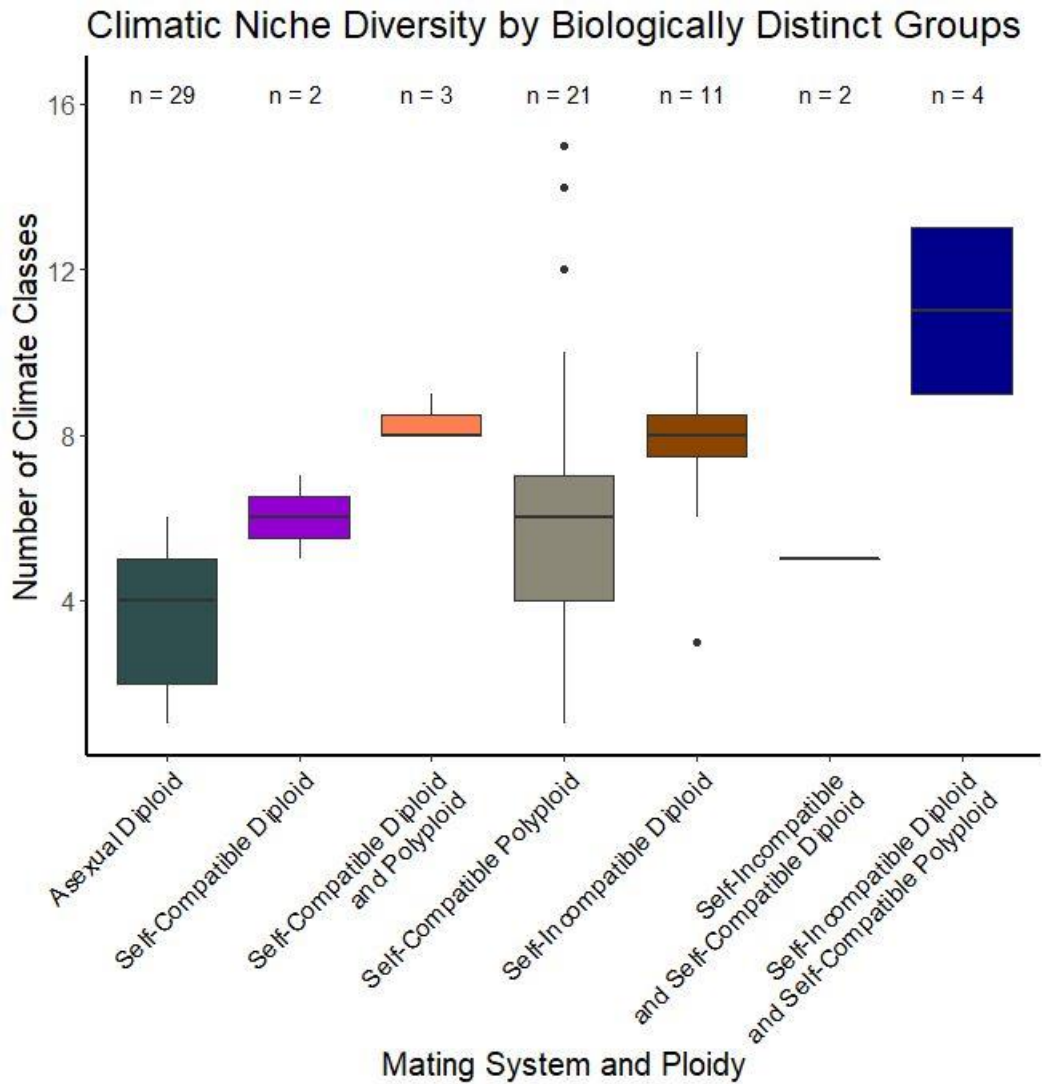
## Figures and Tables

**Figure 1.** Time-calibrated uncorrelated relaxed molecular clock phylogeny with outgroups and cultivated varieties of potato included as generated with BEAST2.

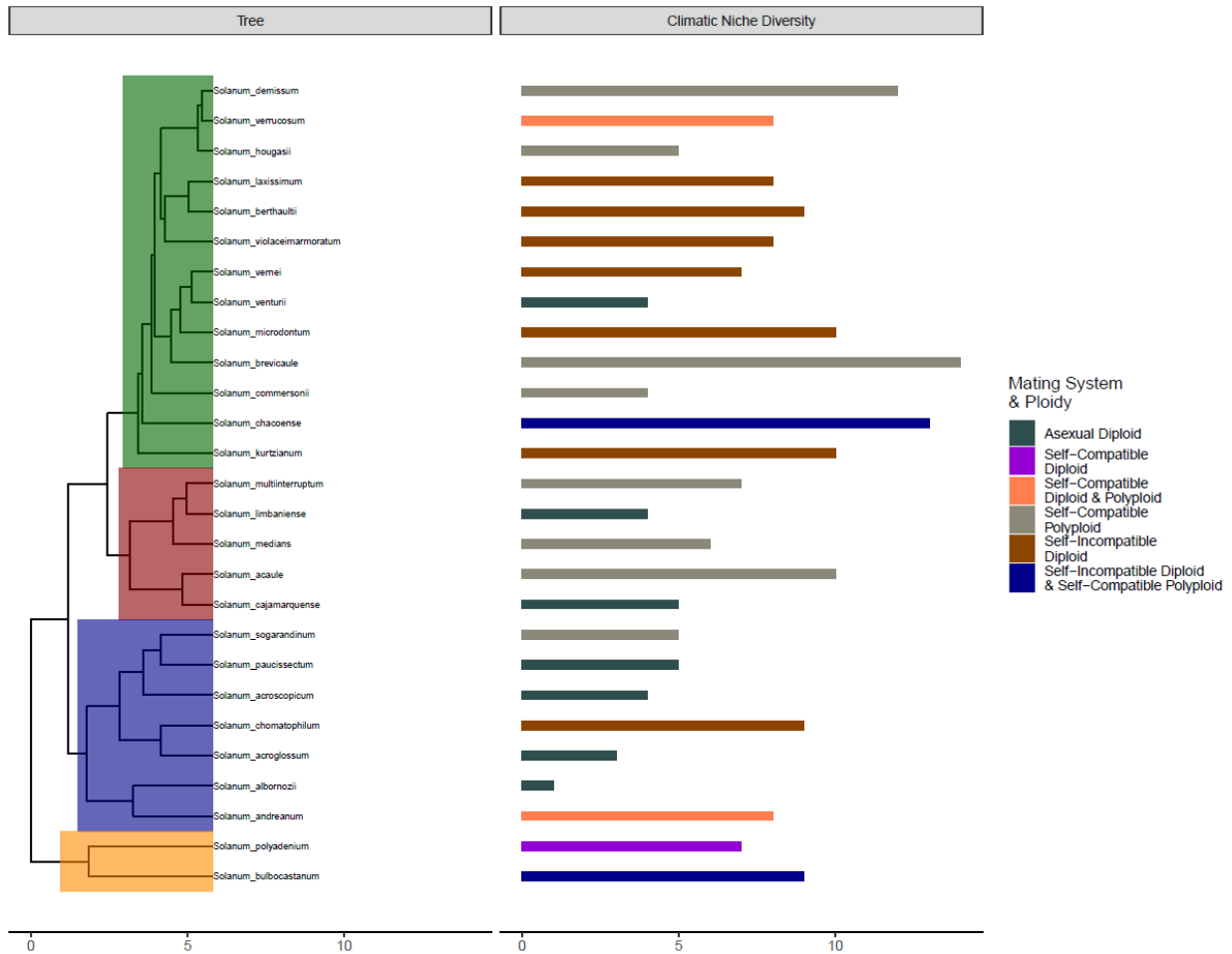




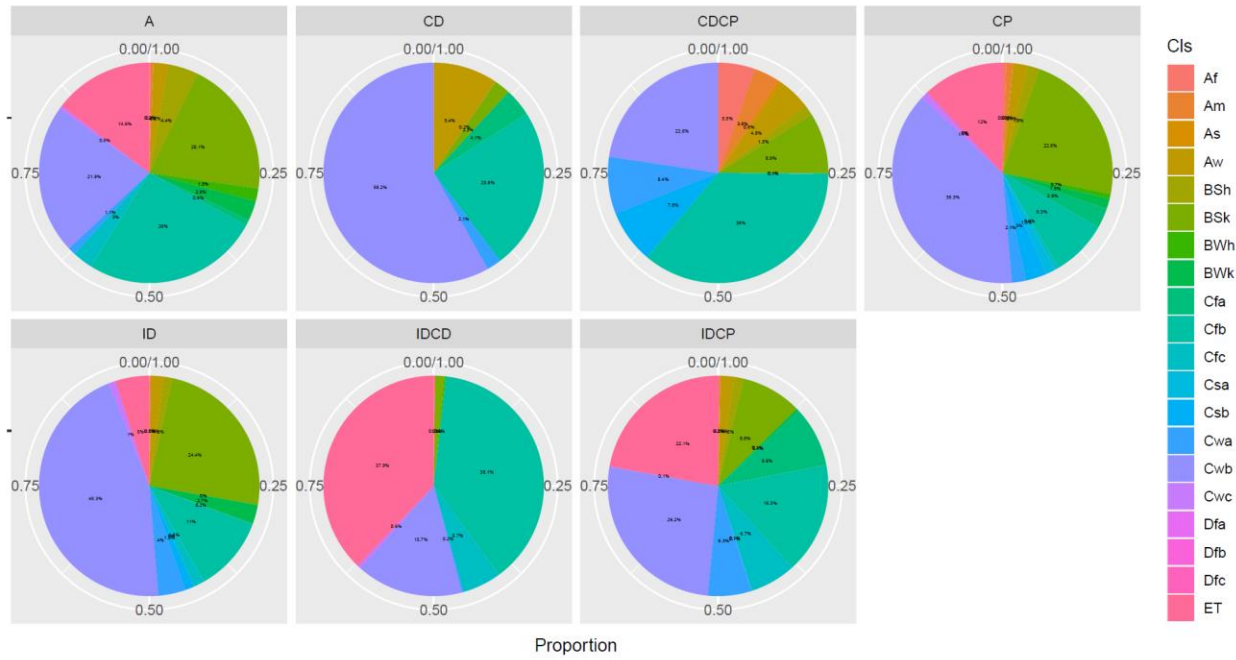
**Figure 2.** Boxplot of niche diversity by breeding system and ploidy interaction in potato wild relative species. Many species exist containing multiple subpopulations with differing biological factors, as seen by combination of such factors on the x-axis.



**Figure 3.** Dual figure with time-calibrated molecular clock phylogeny (left) with climatic niche diversity (i.e., number of climate classes occupied) (right). On the left side, the x-axis scale bars represent millions of years and the background coloration of the phylogenetic tree highlights widely accepted clades of *Solanum* section *Petota*. On the right side, the number of climate classes a species occurs in is represented by the size of the horizontal bar and measured with the x-axis scale bar and the coloration of the horizontal bars represent species biological attributes as breeding system with ploidy.



*Figure 4. Pie chart of climate class proportions by breeding system/ploidy combinations.*



**Table 1.** Results from the linear model for climatic niche diversity following Gaussian distribution. The number of discrete climate classes in which each taxon can occur (i.e., a proxy for niche breadth) is the response variable, Climate Niche Diversity. The predictor variables are combinations of ploidy and breeding system for each species, which were coded as dummy variable interaction terms: self-incompatible diploid, self-compatible diploid, self-compatible asexually propagating polyploid, and unknown breeding system asexually propagating diploid. Values of reported in column 2 are the maximum likelihood estimates and standard error of the estimates (surrounded by parentheses).

| <b>Ordinary Least-Squares Results</b> |                            |
|---------------------------------------|----------------------------|
|                                       | <i>Dependent variable:</i> |
|                                       | Climatic Niche Diversity   |
| Self-Incompatible Diploid             | 3.134***<br>(0.734)        |
| Self-Compatible Diploid               | 0.569<br>(1.021)           |
| Self-Compatible Polyploid (Asexual)   | 3.624***<br>(0.789)        |
| Asexual Diploid                       | 0.883<br>(0.992)           |
| Intercept (MLE)                       | 2.813***<br>(1.006)        |
| Observations                          | 72                         |
| R <sup>2</sup>                        | 0.426                      |
| Adjusted R <sup>2</sup>               | 0.392                      |
| Residual Std. Error                   | 2.493 (df = 67)            |
| F Statistic                           | 12.424*** (df = 4; 67)     |
| <i>Note:</i>                          | * ** *** p < 0.01          |

**Table 2.** Results from phylogenetic linear models for climatic niche diversity following Brownian motion. The number of discrete climate classes in which each taxon can occur (i.e., a proxy for niche breadth) is the response variable, Climate Niche Diversity. The predictor variables are combinations of ploidy and breeding system for each species, which were coded as dummy variable interaction terms: self-incompatible diploid, self-compatible diploid, self-compatible asexually propagating polyploid, and unknown breeding system asexually propagating diploid. Values of reported in column 2 are the maximum likelihood estimates and standard error of the estimates (surrounded by parentheses).

| <b>Phylogenetic Least-Squares Results</b> |                                    |
|---|------------------------------------|
|   | <i>Dependent variable:</i>         |
|   | Climatic Niche Diversity           |
| Self-Incompatible Diploid                 | 3.984***<br>(1.036)                |
| Self-Compatible Diploid                   | 1.856<br>(1.536)                   |
| Self-Compatible Polyploid (Asexual)       | 2.574*<br>(0.975)                  |
| Asexual Diploid                           | -2.332<br>(1.620)                  |
| Intercept (MLE)                           | 6.426***<br>(1.670)                |
| Sigma <sup>2</sup>                        | 8.088e-09<br>(2.967e-09,1.067e-08) |
| Sigma <sup>2</sup> Error                  | 4.497<br>(1.650,5.933)             |
| Observations                              | 27                                 |
| R <sup>2</sup>                            | 0.527                              |
| Adjusted R <sup>2</sup>                   | 0.441                              |
| Residual Std. Error                       | 4.761 (df = 22)                    |
| Parametric Bootstraps                     | 100                                |
| Note:                                     | *p**p***p<0.01                     |

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## **Chapter 2: Crop wild relatives of potato may bolster its adaptation to new production niches under future climate scenarios**

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## Abstract

Food production strategies and patterns are being altered by climate change. Enhancing the adaptation of important food crops to novel climate regimes will be critical to maintaining world food supplies. Climate change is altering the suitability of production areas for crops such as potato (*Solanum tuberosum* L.). Future productivity, resilience, and sustainability of this crop will be dependent on breeding for climate adaptation, including through the introgression of novel traits from its wild relatives. To better understand the future production climatic envelopes of potatoes, and the potential of its wild relatives to contribute to adaptation to these environments, we estimated the climate of potato in four future scenarios and overlapped the current climate of 72 wild relative species and potato with this future climate. We discovered a shift of up to 12% by potato into novel climate by 2070 and varying magnitudes of overlap by wild relatives with potato, primarily driven by the extent of endemism. To address the threat of change to novel climate and with the wealth of data available for the agrobiodiversity in potato wild relatives, we systematically developed a prioritization value inspired by the logic of the breeder's equation for locating potentially beneficial species possessing local adaptability, climatic plasticity, and interspecific crossability. In doing so, 26 unique species by discrete climate combinations are found, highlighting the presence of unique species to use in adapting potato to the local climate. Further, the 20 highest prioritized values belong to diploid species, enforcing the drive to shift into diploid breeding by the potato research community, where introgression of the local climate adaptability traits may be more streamlined.

## Introduction

Potato (*Solanum tuberosum* L.) is the fourth most widely cultivated crop globally and the most important tuber for human consumption (>1 billion people annually; FAOSTAT, 2017). The tubers of potato provide a rich and complex source of carbohydrates and essential nutrients, including dietary fiber, vitamins, minerals, protein, and antioxidants (Bach et al. 2012). Potato thrives in a relatively narrow climate niche, for example, tuberization has been empirically shown to diminish at temperatures above 17 °C, negatively impacting productivity (Stol et al. 1991; Haverkort 1990, Hijmans 2003). Future yield projections under climate change indicate a likely production decline in major potato growing regions (Raymundo et al. 2018, Dahal et al. 2019). Changes in potato agronomic practices (e.g., pesticides, fertilizers, and irrigation) have increased the geographic range of production and production per unit area (Hijmans 2001, Hijmans 2003, Murchie et al. 2009, Devaux et al. 2014). Such agronomic practices may help mitigate the impacts of climate change induced production decline and crop improvement can champion these efforts by providing new crop varieties that are more resilient to abiotic stresses.

Potato breeding has generally seen steady improvement with occasional flurries of activity, one such time of rapid improvement was after the late blight epidemics of the 19th century (Jansky and Spooner 2018). Most selections were made from open pollinated populations as specific crosses of cultivars were rarely successful until the mid-20th century (Krantz 1924, Krantz 1946, Comai 2005, Jansky and Thompson 1990, Bradshaw and MacKay 1994). Improvement in potato yield in the last century was mostly due to agronomics while improvements in quality traits have been attributed to genetics. Potato is a clonally propagated, autotetraploid crop with a narrow genetic base compared to the wild relatives (Spooner et al., 2014). These factors continue to make breeding difficult despite recent efforts to incorporate new diversity (Jansky 2009), including introgression with potato wild relatives (hereafter PWR). Modern cultivars of potato possess relatively little

difference in the percentage of heterozygous loci nor the frequency of homozygous from cultivars developed in the past two-centuries (Hirsch et al. 2013, Vos et al. 2015). Additionally, cultivar turnover is very slow in many regions, for example with cultivars in North America being grown for 40-50 years (reviewed in Singh et al., 2019). Using PWR has helped to introduce genetic diversity and valuable agronomic traits, most importantly disease resistance into breeding lines (Hijmans 2001; Jansky et al. 2013; Castañeda-Álvarez et al. 2015; Zhang et al. 2017).

PWR are a highly diverse set of species found in *Solanum* section *Petota* (Castañeda-Álvarez et al. 2015). These species have a range of ploidy and meiotic behavior (disomic, polysomic, and mixed-somic inheritance), occasionally causing meiotic problems when crossed with the crop (Key 1970). Many attributes of the PWR have been defined, including their ploidy, mating system, germplasm classification, endosperm balance number, phylogenetic relationships, and geographic ranges in order to operationalize their use in breeding (Hijmans 2001, Spooner & Hijmans 2001, Spooner & Hettersheid 2007, Castañeda-Álvarez et al. 2015, Zenil-Ferguson et al., 2019). The goal of plant breeding is to move the population mean of a given trait to a more beneficial value for the particular human use it is intended, the speed with which this can be done is often measured using the breeder's equation (Lush 1943), which conceptualizes efficiency after accounting for genetic variance and selection intensity. The framework has not been explored in the context of climate change projections and crop wild relatives.

Global food security is threatened by climate change, impacting production and land use change (Foley et al., 2011; Ramankutty et al., 2018; Mehrabi et al., 2020). Historic climatic events and shifts have placed pressure on crop cultivars by creating novel abiotic and biotic stresses (Lesk et al. 2016). Future projections provide a way to create realistic assessments of means and variances of future climate scenarios. Adaptation strategies include: (i) sourcing crop populations (e.g. landraces,

varieties) from different global geographic regions matching future projected climate, (ii) assessing crop wild relatives for naturally evolved adaptations, (iii) defining replacement crops to be cultivated, (iv) defining different agroecosystems for existing crops, (v) substantially changing agronomic practices such as row spacing, irrigation and planting date, and (vi) abandoning current production locations with human population moving to areas amenable to current practices/cultivars (Burke et al., 2009; Ramirez-Villegas and Khoury, 2013; Pironon et al., 2019; Sloat et al., 2020; Heider et al., 2021). Despite research exploring the potential for shifts in existing production zones or towards zones forecasted for potato production compatibility (Leemans & Solomon 1993, Hijmans 2003), such shifts present tradeoffs through encroachment on natural ecosystems and through limiting human livelihoods (Tanentzap et al. 2015, Smith et al. 2014). Therefore, the least disruptive option is utilizing agrobiodiversity for adapting crops to the changing environments with conventional breeding techniques (Borlaug 1983, Jansky et al. 2013, Dempewolf et al. 2017). Utilizing wild relative species, as well as landrace and heirloom varieties, provides a mechanism to alleviate the abiotic stresses expected with climatic shifts through evolved traits including tolerance to salinity, drought, and temperature extremes (Bailey-Serres et al. 2019, Ramankutty et al. 2018). This has led to large redundancy and overlap in personal (e.g., breeding programs) and institutional collections (e.g., germplasm banks), resulting in the overcollection of some species and under collection of others (Dempewolf et al., 2017).

Here we focus on assessing crop wild relatives for naturally evolved adaptations, which is broadly focusing on agrobiodiversity, which has a recognized role in mitigating the threat to crops (Dempewolf et al., 2017). The uncertainty of future climatic conditions creates a situation where breeders must efficiently and effectively prioritize the best potential species to create interspecific populations from and to ameliorate shift-induced stress on production. Therefore the objectives of this study were to (i) model the shift in climatic conditions expected for potato in the future (2050

and 2070) at a global scale, (ii) model the current climate niche of 72 PWRs, (iii) assess overlaps between the climate niches of PWRs and the novel/future conditions expected for potato, (iv) propose a formalized approach to prioritize PWRs for use in breeding based on their potential for future climate adaptation in specific climatic zones (Pironon et al. 2020). Conceptually, this is similar to envirotyping (Xu, 2016) and enviromics (Resende et al., 2020), but instead of working with breeding populations, here crop wild relatives are explored.

## Materials and Methods

### *Data Acquisition*

Potato production occurrences ( $N = 726,103$ ) were compiled from land use census data at a  $\sim 5$  arc-min resolution in 2000 (Monfreda et al. 2008), while occurrences for the 72 PWR ( $N = 37,250$ ; Table 1) were compiled from previous gap analysis that prioritized PWR (Castañeda-Álvarez et al. 2015). Climate data were retrieved from WorldClim 2.0 (<https://www.worldclim.org/data/cmip6/cmip6climate.html>) for the years 1970-2000 (hereafter “current climate”, Fick and Hijmans, 2017) at a 5 arc-minutes ( $\sim 10$ km) resolution (Eyring et al. 2016). Future climate projections are based on the sixth assessment report (AR6) of the Intergovernmental Panel on Climate Change (IPCC) that uses various shared socioeconomic pathways (SSPs) for different global climate models (GCMs). Nineteen variables provided by WorldClim were utilized to ensure full capture of mean and variance of temperature and precipitation conditions across and between seasonal shifts for potato and each of its PWRs (Table 2). The same variables were collected for the 2050 and 2070 time periods (averages for 2041-2060 and 2061-2080, respectively) according to two shared socioeconomic pathways (SSPs) of SSP2-4.5 (considered a medium effort to curb emissions) and SSP5-8.5 (considered low to no effort to curb emissions) and eight GCMs (global climate models). The eight GCMs were BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0. Current and future climatic information were extracted for each potato and PWR occurrence point using the `extract` function in the raster package of R. Data for the Köppen-Geiger climate classes of PWR and life history traits were derived from Fumia et al. (2020). The Köppen-Geiger divides climate regimes into a discrete three-tiered system (five main, 30 sub and sub-sub tiers) based on main climate, seasonal precipitation, and temperature (reviewed in Rubel and Kottek,



2010). Further, the regression coefficients for climate niche diversity as well as phylogenetic relatedness were sourced for PWR from Fumia et al. (2020).

### *Climate comparisons*

We performed principal component analysis (PCA) to identify the climate niches of the cultivated potato at current future time points and compare to the current climate niche of its 72 wild relatives using the 19 bioclimatic variables using the R packages *ade4*, *grDevices*, and *sp*. Climate niches were built using convex polygons around the occurrence points of each species in the principal component climatic space from PC1 (46.4% variance explained) and PC2 (22.2% variance explained) in the joint analysis of species. The technique of convex hull was chosen for quantifying the niche space over alternatives as it does not rely on point density (important because occurrence point sampling is uneven in geographic space) and is conceptually simple and readily interpretable. However, this technique is sensitive to outliers; therefore, the analyses were repeated discarding six different selections of outliers based on Mahalanobis distances (values ranging from 5 to 10) between each occurrence point and the centroid of the species climatic niche, as in Pironon et al. (2019). We estimated the current and future climatic conditions of potato and the current climatic conditions of the 72 PWRs. To estimate the impact of life history traits, species with the same mating system/ploidy combinations were first aggregated, then polygons were drawn around the combined data. The climatic change of potato was estimated as the percentage of the total area of the polygon representing future climatic conditions that is not intersected by the total area of the polygon representing current climatic conditions. We described novel climate as the expected future climate space that is not intersected by the current climate space, indicating a climatic zone of high insecurity facing future potato production. We then analyzed how current PWR climatic niches

overlap with this novel climate space in order to estimate the potential contribution of each PWR to potato's adaptation under climate change.

### *PWR Prioritization Score*

We developed a PWR prioritization (PWRP) score inspired by the logic of the breeder's equation (BE) (Lush 1943, Lynch and Walsh 1998, Walsh and Lynch 2018, Bernardo 2020). Specifically, we conceptualized the PWR species niche overlap with future and current potato climatic conditions at different time points as phenotypes, analogous to the response to selection, which we call climate response potential (Figure 1). Considering this, we calculated the PWRP utilizing the format of the BE (for full explanation of each terms relationship to the traditional BE see Figure 1):

$$\textit{Potato Wild Relative Prioritization} = \textit{applicability} * (\textit{environmental plasticity} + \textit{evolutionary history}) * \textit{spread}$$

$$PWRP = a * (ep + eh) * \sigma$$

Instead of having a response in progeny there is a predicted response in a species over time, this presents a potential capacity for climate adaptability and thus a higher score in a specific environment means a higher utility as a donor species, this is represented as *PWRP*. Instead of selection intensity (phenotypic variance selected on) the proportion of a discrete niche (Köppen-Geiger climate class) is conceptualized as the phenotype which varies showing future potential adaptability, represented as *applicability* (*a*). The Köppen-Geiger class system (Rubel and Kottek 2010) provides climate zones that are useful when defining the range of a particular breeding program and knowing the discrete class provides a shorthand for localization of valuable breeding germplasm. Therefore, *applicability* (***a***) serves as a honing value from the current occurrence of a given PWR in a specific discrete climate class as a percentage of occurrences in that class over the total number of occurrences of that species (Köppen-Geiger Climates, Figure 2). Further, to

highlight the ability to localize valuable germplasm this discretizing allows for a correction of the PWRP response to represent 0 where a species does not exist and would be unlikely to offer phenotypic advancement to cultivated potato in that climate, to greater than 0 where the species solely exists in that specific climate.

Instead of heritability we have a combination of the crossing potential and the plastic response in different time periods as the correlation of individual PWR overlap with current and overlap with future climate niche of potato. *Environmental plasticity* (*ep*) represents the correlation between the niche overlap of PWR over the current climate of potato with the niche overlap of PWR over the future forecasted climate of potato (adjusted for each SSP and year combination). Due to the interspecific nature of potential crosses, we adjust the correlation between timepoints with crossability using two aspects: (1) to adjust for the evolutionary role in climatic diversity we use the regression coefficient for niche divergence among of PWR with different life history trait interaction (see Fumia et al. 2020); and (2) to adjust for the evolutionary role in crossability we use the chloroplast genome genetic distance between all PWR and *S. tuberosum* (Fumia et al. 2020), representing the *evolutionary history* (*eh*). The *evolutionary history* (*eh*) represents the regression output of life-history trait influence upon climatic variation as specifically the intercept + or - the slope value by a PWRs life-history trait combination (mating system by ploidy) (Fumia et al. 2020). Additionally applied in *eh* is phylogenetic distance, calculated as the Bayesian predicted plastid genomic distance from the cultivated potato (*S. tuberosum*) from Fumia et al. (2020), this metric could be replaced with any metric of phylogenetic relatedness. Instead of additive genetic variance, we conceptualize this as the variance associated with *environmental plasticity* (*ep*) and *evolutionary history* (*eh*), representing the *spread* ( $\sigma$ ). *Spread* ( $\sigma$ ) accounts for the variation in attributes of *ep*, as determined by the standard deviation among the different GCMs used in climate projections, and *eh*, as determined by the standard deviation of the regression intercept + or - the standard deviation of the slope value.

## Results

Under future projected climates there is both a clear overlap between current and future climates of potato by mating system/ploidy and novel climate space being inhabited (Figure 3). Following the SSP 4.5, we predict a 7.0% change in the climate niche of potato by 2050, increasing to 8.4% in 2070. Following a scenario of low effort to curb greenhouse gas emissions (SSP 8.5), we find an 8.7% change in the climate niche of potato by 2050, increasing to 12.5% in 2070. Considering global climatic shifts, ~6-12% of the future projected climate space of potato will be novel, depending on the climate model and emission scenario considered. The above changes in potato niche are primarily shifts along PC1, mostly formed by temperature variables (Table 2). This novel climate space is partially occupied by PWR species that possess self-compatible, diploid populations, which in general have the largest ranges and exist in novel climates relative to the current extent of potato. These self-compatible, diploid PWRs exist in the current climate primarily identified by lower PC1 (temperature) and PC2 (precipitation) values (Table 2).

The range in the size of climate space varied from the narrowest PWR (*Solanum gracilifrons* Bitter) found in a single small valley near Colcabamba, Peru, to the broadest climate niche of potato, an effect of domestication. PWRs exist in a large number of discrete climate classes (Figure 2), ranging from narrow endemic species occurring in single climate classes (e.g., *Solanum salasianum* Ochoa) to those which exist in over half of the major biomes of earth and 15 climate classes (e.g., *Solanum chacoense* Bitter). The current climatic niche of PWRs shows substantial variation between the predicted novel climates from the general climate models (GCMs) in the future (2050 and 2070) in the different emission scenarios (SSP 4.5 and 8.5) when overlapped with current and future niches of potato production. As expected, there is more shift in the climate niche at the later time point 2070 and under the more severe emission scenario SSP 8.5 (Figure 4). The largest range seen among

the examined species is the domesticated potato. The range expansion of the domestic compared to the PWR can be observed in the number of Köppen-Geiger climate classes where potato occurs relative to PWR species (Figure 2) as well as the total area covered within the climate spaces (Figures 3, 5, and 6).

Under future projected climates there is clear overlap of novel climate space by individual PWRs (Figure 3b). In SSP 4.5 in 2050 there was an average overlap of 47.5% by PWRs over the future climate niche of potato, decreasing to 47.0% in 2070. In SSP 8.5 in 2050 there was an average overlap of 47.1% by PWRs over the future climate niche of potato, decreasing to 45.7% in 2070. PWR, specifically the top-8 identified (Figure 7), exhibit the adaptation to a higher degree of lower PC1 and PC2. Here the species that show the most change and most potential for future use in novel space are the species *S. colombianum* and *S. andreaeanum*, both possessing populations of self-compatible diploids as well as driving the novel climate space of the secondary gene pool (Figure 3c).

The matrix of prioritization values (PWRP) shows clear variation in PWR regarding utility for breeding with potato for adaptation to climate change (Figure 8 and 9; Table 3). The species that showed the best potential for use in adaptation to unique climates were *Solanum neocardenasii*, *Solanum incasicum*, and *Solanum pillabuatense* (Table 3). However, when the end goal shifts, the species with the highest overall PWRP when compared to all other species shifts to *Solanum colombianum* (Table 4). As expected, these species are associated with the Oceanic climate (Cfb) or Subpolar oceanic climate (Cfc), characterized by narrow annual temperature ranges (Rubel and Kottek 2010). The next top species are found in extremely different climates. *Solanum neorossi* and *Solanum neovavilovii* possess high PWRP values associated with climates Subtropical highland climate (Cwb) and Polar tundra (ET), respectively (Table 4). Furthermore, when looking at the species with the top 20 highest PWRP, all species are either diploid or possess diploid populations. Additionally, when

considering the top two species per Köppen-Geiger climate (17 discrete climates), there are 26 unique species identified for applicability in any given climate (Table 3). Additionally, more than half of the 80 highest valued PWRPs correspond with species identified for Temperate oceanic (24) and Subtropical highland (21), highlighting the agrobiodiversity available for localized crop improvement in these discrete climate niches (Table 4) where only 10% of current potato production occurs, 7.7% and 2.4% respectively (Figure 2). Broadly useful species, identified in multiple climates as viable options, include *S. andreaeanum*, *S. brevicaule*, *S. chacoense*, *S. colombianum*, *S. bongasii*, and *S. longiconicum*; furthermore, PWR do not occur in every discrete climate of potato, however, the similarity of discrete climates along PC1 and PC2 can be identified for approximate matches (Table 5).

## Discussion

### *Climatic shift and adaptation strategies*

The projected shifts in climate envelopes introduce hurdles for the sustainable production of potato. There are currently 370 million tonnes and 17 million hectares of potato in production (FAOSTAT 2017). If we consider the worst-case scenario for 2070 and assume production is evenly distributed across the climate polygons, there will be a maximum of roughly 44 million tonnes, or 2.1 million hectares, of potato that will need to be produced in a new climate given the expectation of 12% of production potato being shifted from current to 2070. This shift is similar to other major crop species such as sunflower (Mehrabi et al., 2019) and common bean (Ramirez-Cabral et al., 2016). Shifting climate can be addressed through either bringing new land into production or intensifying production on the remaining land, creating a change in the production system where adapted cultivars will be a key component. The shift is about 10 million tonnes more than the international production of dry beans and roughly one-third of the international banana production area (FAOSTAT 2017). Potato future climate shifts occur along a lower PC1 (temperature) and higher PC2 (precipitation) gradient while PWRs primarily exist in lower PC1 and lower PC2 (Figure 3, 5, and 6) gradients. Therefore, PWRs may more likely provide the ability to ameliorate stresses associated with lower climatic shifts along PC1 (temperature) and PC2 (precipitation). A limitation of our analysis is the assumption that production will remain in the same location and same production intensity. This assumption was made based on the specialized equipment and processing facilities that accompany large scale potato production. Historically, there have been production shifts (e.g., New York to Idaho in the United States; Lucier 1991), but such shifts require large capital investment, often being driven by outside infrastructure and are therefore difficult to predict. The least disruptive option for growers and processors would be to use PWR for genetic

improvement of production cultivars to increase productivity on existing cultivated lands rather than expanding production to new areas (Dias et al., 2016).

### *Agroecological Niche and Prioritization of Potato Wild Relative Species*

A consideration when prioritizing agrobiodiversity is the identification of traits that are useful to agricultural production in specific regions and agroecosystems, these can differ from those that provide adaptability to populations in natural ecosystems (Fumia et al. 2020). In this study, the traits influencing climate adaptability and plasticity as well as crossability to cultivated species were combined in the prioritization, similar conceptually to envirotyping (Xu, 2016) and enviromics (Resende et al., 2020). However, rather than finding the best cultivar for an environment here we prioritize species with localized climate adaptation for specific climate/production niches found throughout the world (Table 3, Figure 8 and 9). Different global regions have different potential donor species for abiotic stress adaptation, for example, *S. colombianum* was identified as a useful donor species in Af (Tropical Rainforest) and Csb (Warm-Summer Mediterranean), as it likely contains the potential to provide adaptability to increased temperatures thus helping to alleviate diminished tuberization and yields that have been documented under high late season temperatures (Stol et al. 1991; Haverkort 1990, Hijmans 2003). Further, in coastal regions where increased salinity is expected via salt-water inundation, localized adaptability from *Solanum neocardenasii* in Cfb (Temperate Oceanic) could be introduced to ameliorate the abiotic stress. These examples are generalizable to any climate where there are data, in each case a donor species can be selected for generating locally adapted lines in an effort to curb current and future local niche stresses to production. However, selection can be interpolated with associating climate likeness in principal component space (Table 5). This score provides the breeder with a starting-point species identified to have the highest plasticity, localized adaptability, and crossability based on phylogenetic distance.



Moreover, prioritized species can be further filtered to account for known biotic resistances, similar to sunflower prioritization (Mehrabi et al. 2019). An example would be selecting the species (*S. colombianum* and *S. andreaeanum*) with the highest climate plasticity (e.g., largest climate niche) but adjusting the selection to documented *Phytophthora infestans* resistance found in *S. andreaeanum* while avoiding the overwhelming susceptibility to the disease in *S. colombianum* (Khuitti et al., 2015). While this study explored potato, the method can be expanded to any crop.

#### *Use of PWR in Potato Breeding: Diploid Potato is the future*

Historically, interspecific breeding, while used was limited due to the creation of populations without local adaptability and with meiotic instability, leading to cycles of recombination to remove linkage drag and increasing the length of time needed to introgress a trait (Jansky and Peloquin 2005, MacKay 2005, Bradshaw and MacKay 1994). Moreover, this has led to the development of complex crossing schemes requiring additional generations before testing (Peloquin et al., 1999; Hijmans et al. 2007; Köhler et al. 2010). One potential way to overcome this is to work with species prioritized for local adaptation and to work at the diploid rather than tetraploid level. The top prioritized PWR are diploid, however, cultivated potato is tetraploid with polysomic inheritance, leading to complex segregation patterns during breeding. This means that additional resources must be expended to find favorable genotypes (McCord et al. 2012, Little 1945 & 1958). Further, there are additional challenges that occur in interploidy hybridization between PWR and potato, often requiring additional steps such as ploidy reduction, bridge crosses, and re-polyploidization (Peloquin et al. 1989, Ortiz and Peloquin 1991, Serquén and Peloquin 1996, Santini et al. 2000, Jansky 2006). This extended breeding cycle is exacerbated by the standard intensive breeding process of progeny testing (De Jong and Tai 1991). Such challenges suggest that the move toward diploid germplasm (Jansky et al., 2016) should be accelerated to keep within resource constraints and improve response time to

climatic shifts, using the most promising PWR (diploid). Potato breeding is focused on clonal selection, where extreme outliers are important because they can become a cultivar and their outlier nature is not lost through sexual recombination. Since outlier selection is important, breeders rely upon selecting populations that exhibit the greatest phenotypic variation, with diploid populations often expressing larger variation than tetraploid populations (Jansky and Spooner 2018). While there is great potential to breed in diploids more rapidly, there are also problems with increased genetic load and inbreeding depression (Jansky et al. 2016, Bachem et al. 2019), but these could be overcome by creating an inbred-hybrid system (Zhang et al. 2019). Using these diploid PWR as parental species in diploid breeding programs not only increases genetic diversity but introduces climate resilience and plasticity. Increases in the extremes of a segregating diploid population support the production and identification of broadly or specifically eco-adapted individuals. In doing so, interspecific hybrids may possibly be selfed to achieve homozygous climate adaptation traits and thus, significantly decrease the resource intensity currently associated with potato breeding programs. PWR contain species that satisfy these requirements for many different climate classes, in prioritizing by specific class, a short list can be identified that will provide climate adaptability and inform specific breeding designs to reach goals under different temporal constraints. An interesting question for future work would be to identify if the timeframe for de novo domestication of wild potatoes would be faster than introgression due to meiotic incompatibilities, particularly with respect to climate adaptation.

### *Limitations*

Cultivated potato is produced in irrigated and dryland systems, which are not separated in this study. This limitation implies that the large range in climate space of cultivated potato (Figure 1) when compared to PWR is due to a combination of changes in genetics and agronomic practices (e.g.,

irrigation, fertilization, and pest control) which both expand the production niche. Despite this potential overestimation of the climate niche of cultivated potato, the PWRP metric is disentangled from niche size through the use of the correlation between current overlap and future overlap. The interpretation of this is that when species are prioritized using this metric, they are highly likely to hold the abiotic stress tolerance within the climate class of interest. Additionally, although this study uses 72 wild relative species of potato, it does not incorporate the genetic diversity and potential adaptability traits available in landrace varieties, an area ripe for future investigation (Heider et al. 2021). Lastly, PWRP is a metric to improve selection of germplasm for interspecific breeding in a local niche but does not consider how this selection may alter the final potato product from the current local market preference. The goal is introgression of adaptability traits while maintaining quality traits (e.g., texture, color, nutritional value), however, how the theory meets practice requires empirical testing within potato breeding programs.

## **Conclusion**

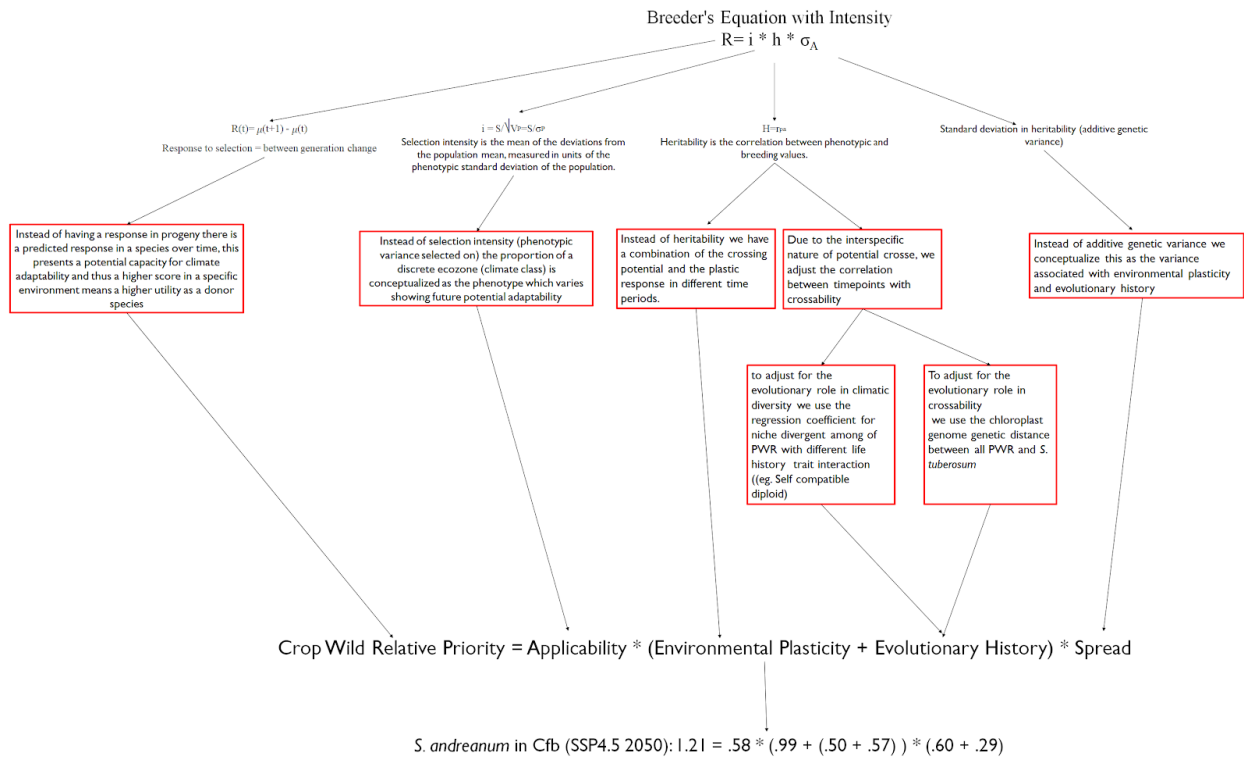
Potato has become a foundational part of the diet of millions of people across the globe. Future cultivation is threatened by an increasingly stochastic climate, in fact here we projected that up to 12.5% of the current cultivated potato climate will shift into novel climates by 2070. This is a tremendous threat to livelihoods and food production; however, we also identified a clear path to future climate adaptation using PWR genetic resources. Actualizing the finding here would be aided by moving breeding systems to diploid germplasm as suggested by Janskey et al. (2016). We have proposed a way of prioritizing species to use in adapting production potato to local climates and specifically finding diploid PWR species, providing support for diploid breeding for streamlined improvement of potato towards abiotic stress adaptability. This may help develop more efficient breeding schemes that will increase the potential of new cultivars to be pre-adapted to the appropriate climate regimes to address the long lag time in agricultural research and development.

## **Acknowledgements**

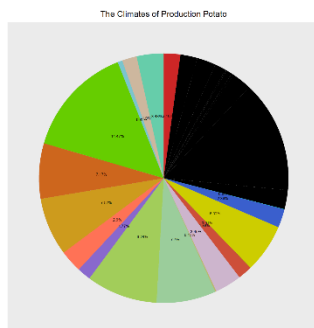
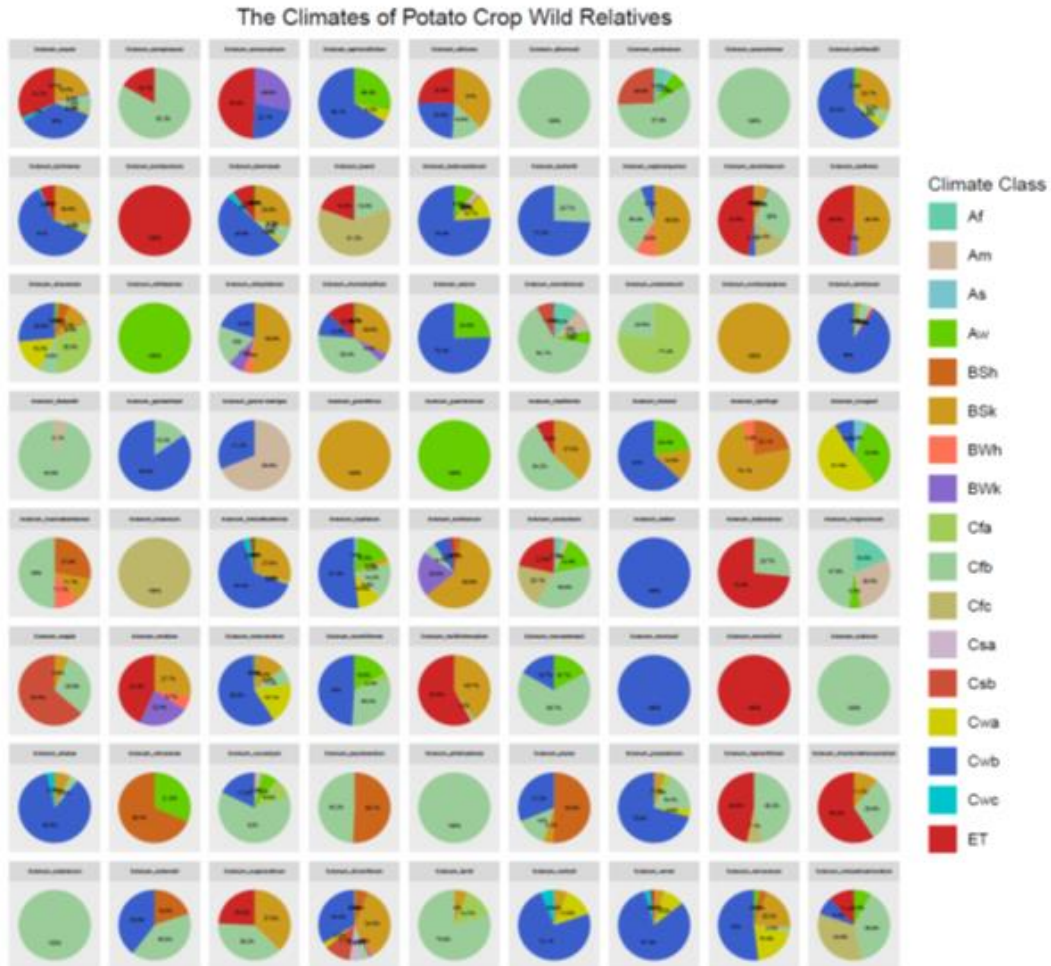
We would like to thank Dr. Walter S. De Jong and Dr. Rosana Zenil-Ferguson for helpful discussion and comments on earlier versions of this manuscript. We would like to thank the Hawaii Agriculture Research Center and the University of Hawaii Office of Sustainability for their support of Nathan Fumia through the Sustainable Agriculture Fellowship, the Information Technology Systems at the University of Hawai'i at Manoa for computer processing support, and access to data via the Centro Internacional de la Papa. We would like to thank Cornell University for supporting the sabbatical of Dr. Michael A. Gore to contribute to this manuscript. C.K.K. was supported by grant no. 2019-67012-29733/project accession no. 1019405 from the USDA National Institute of Food and Agriculture.

## Figures and Tables

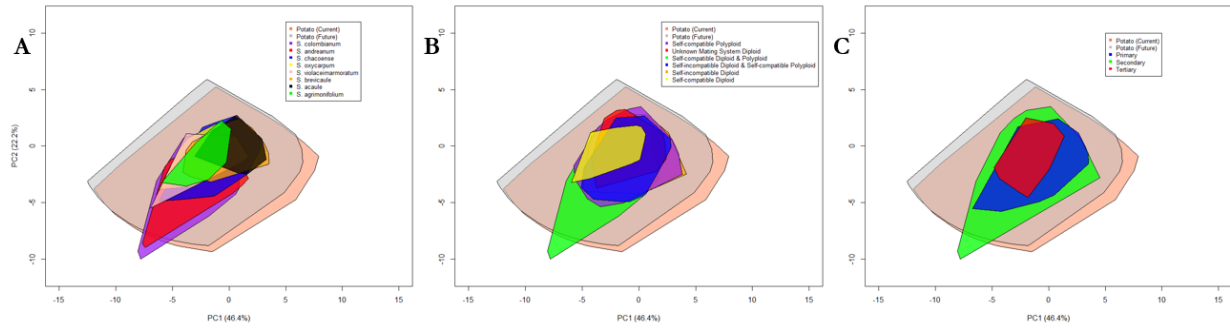
**Figure 1.** Conceptualizing the response to climate change as a phenotype and using breeding logic to identify parental species for crossing in specific environments to create a PWRP. This is a value that is inspired by the breeder's equation (Lush 1943, Lynch and Walsh 1998, Walsh and Lynch 2018, Bernardo 2020). Selection intensity is mimicked by relevance in that a higher proportion of occurrence in a given climate (example is Cfb Oceanic climate) results in a higher relevance to the climate response. To mimic accuracy with environmental plasticity + evolutionary history (taking the place of additive effect of phenotypic value and genetic value) with the information that we have available for potato wild relatives. Environmental plasticity is the phenotype of interest and mimics the traditional phenotypic value by calculating the climate niche overlap with production potato. Evolutionary history plays the part of a traditional breeding value in that it is the additive evolutionary value as opposed to the additive genetic value (using the genetic information we do have such as ploidy/mating system and phylogenetics always bringing it back to the phenotype of interest: climate adaptability). This additive evolutionary value is the additive effect of life history trait on climate diversity plus the phylogenetic relatedness. Spread takes into account the variance associated with the environmental plasticity and evolutionary history.



**Figure 2.** Climate classes each potato PWR is present in followed by the climate classes of production potato. Those climates identified by black color are those that PWR do not occur.

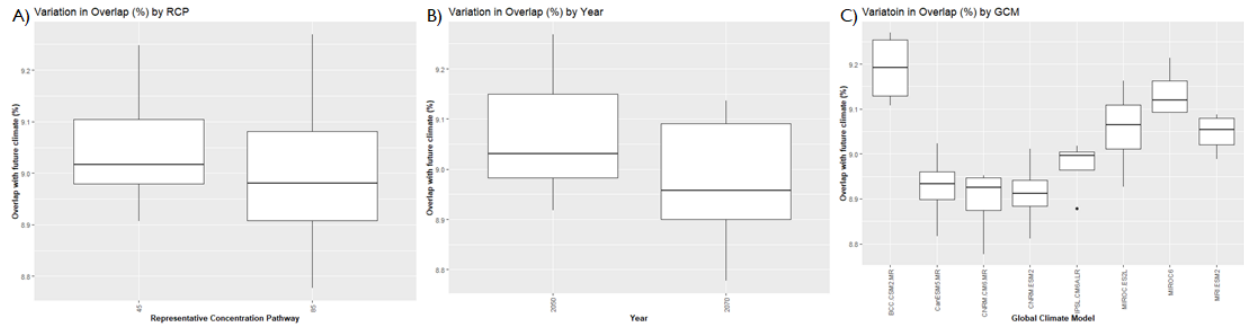


**Figure 3.** Principal component analysis of environmental space of PWR under SSP 8.5 in 2070 grouped as A) top-8 overlapping PWR, B) life history traits, and C) gene pool.

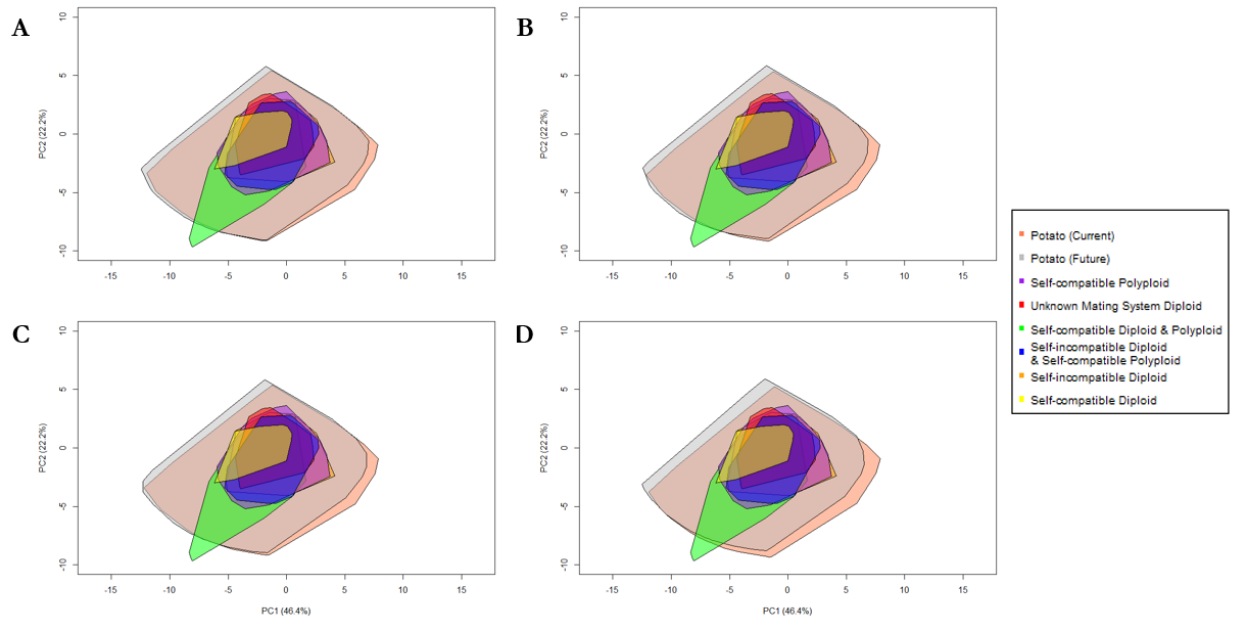




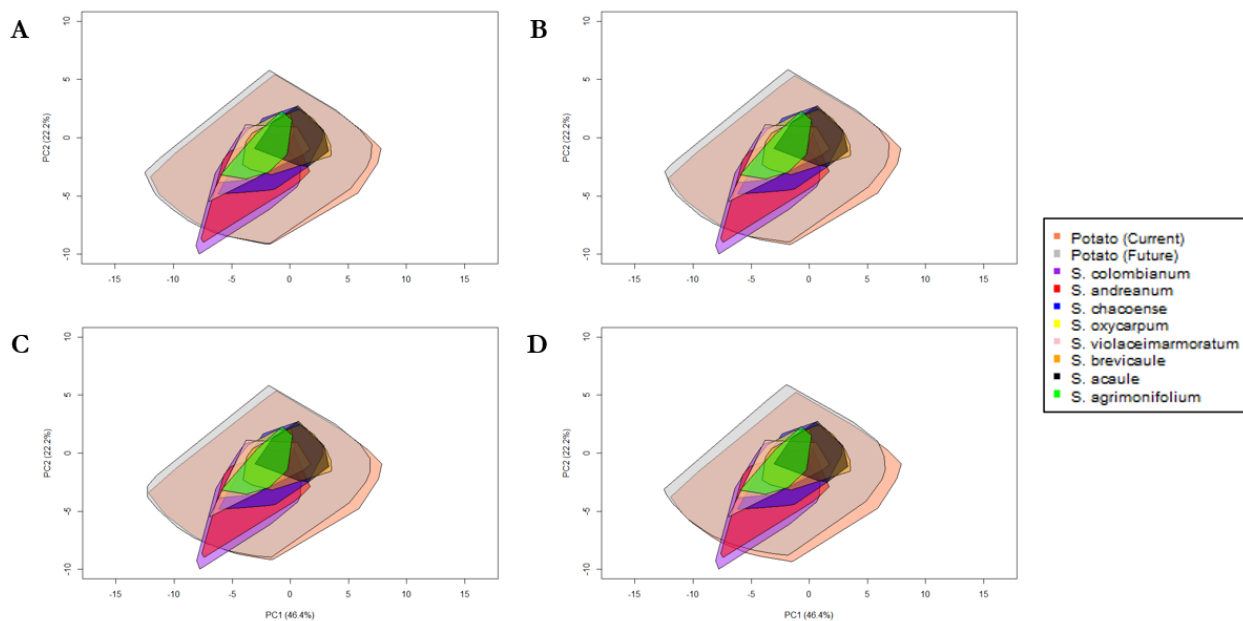
*Figure 4. Differences in Niches by SSP, Year and GCM.*



**Figure 5.** Principal component analysis of environmental space of PWR grouped by life-history trait combinations under A) SSP 4.5 in 2050, B) SSP 4.5 in 2070, C) SSP 8.5 in 2050, and D) SSP 8.5 in 2070.

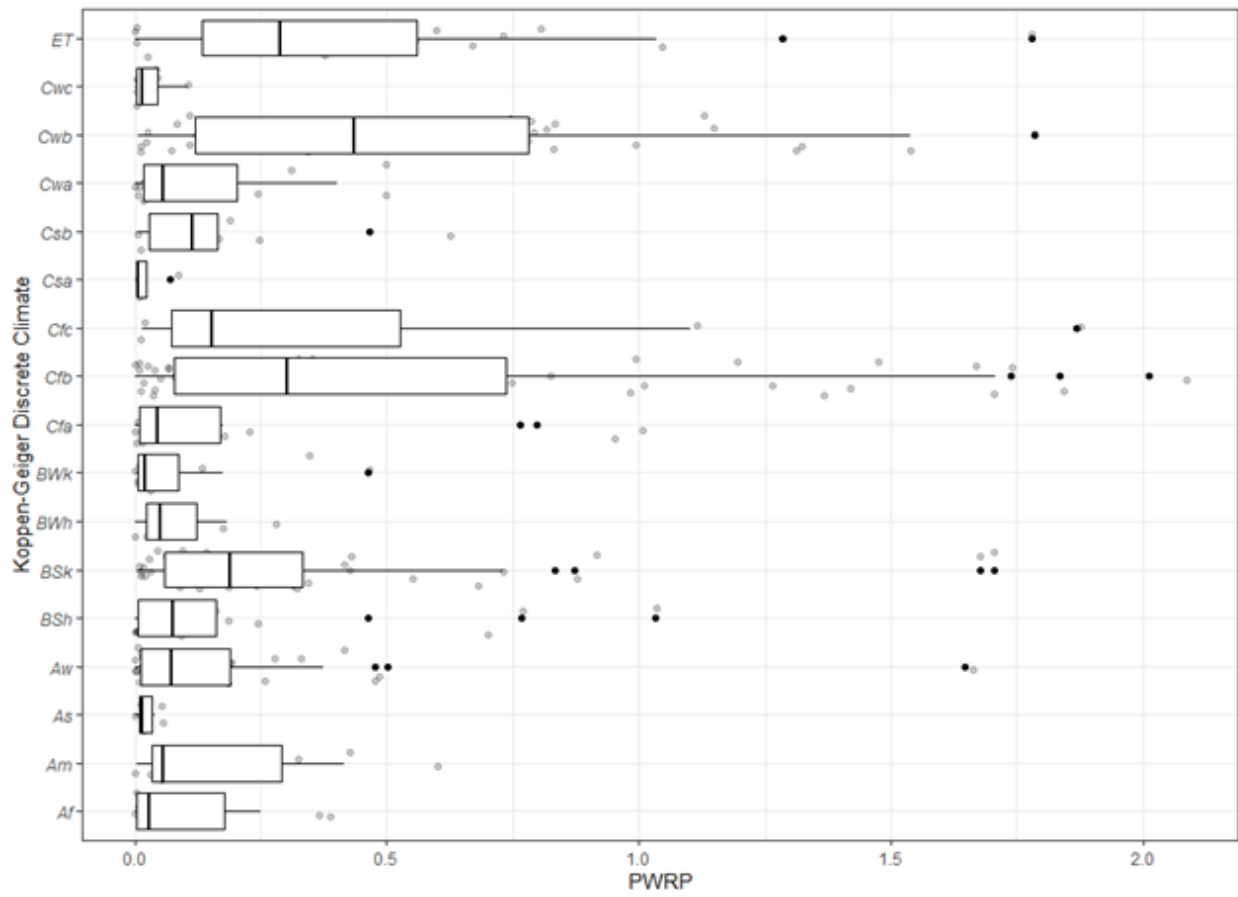


**Figure 6.** Principal component analysis of environmental space of PWR as top-8 overlapping species under A) SSP 4.5 in 2050, B) SSP 4.5 in 2070, C) SSP 8.5 in 2050, and D) SSP 8.5 in 2070.

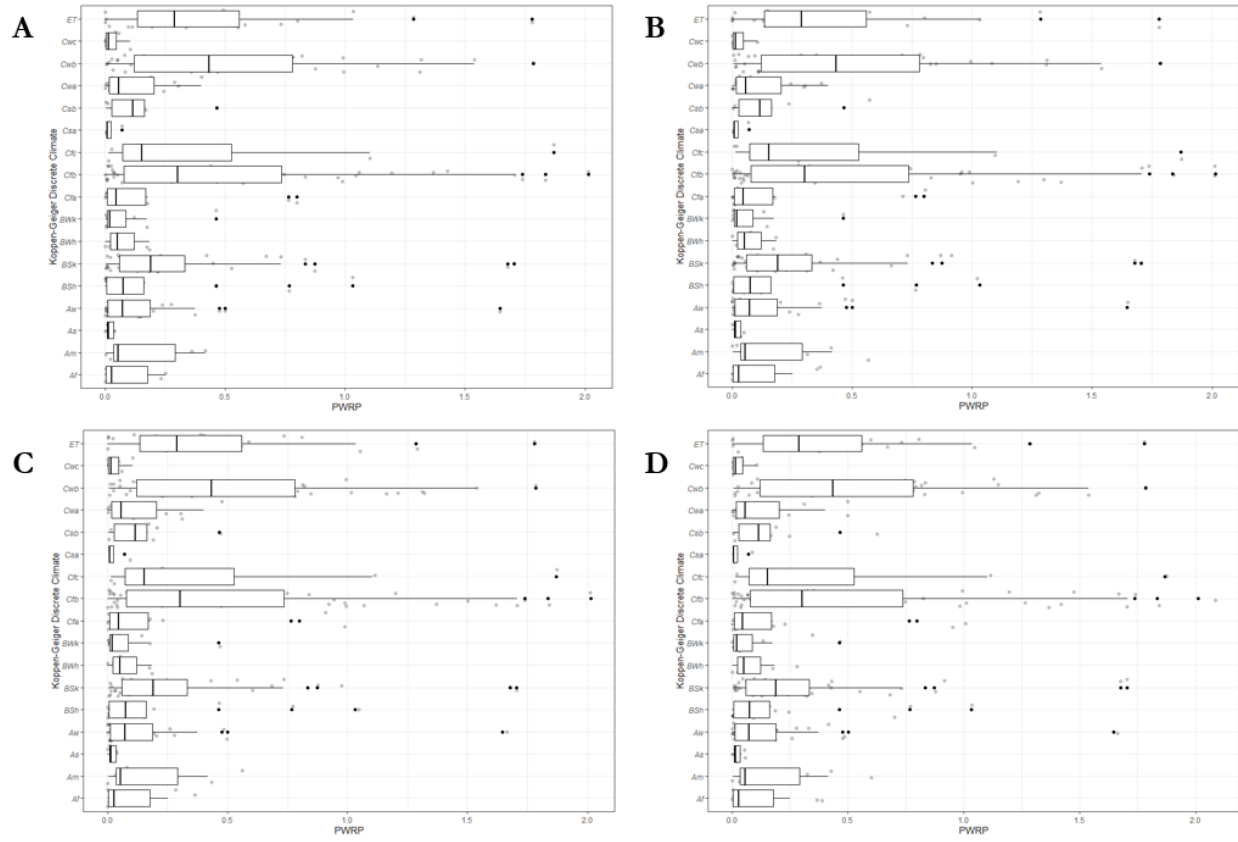




*Figure 8. Boxplot of PWRP for each climate class under SSP 8.5 2070.*



**Figure 9.** Boxplots of PWRP for each climate class for each PWR species, at a) SSP 4.5 2050, b) SSP 4.5 2070, c) SSP 8.5 2050, and d) SSP 8.5 2070.



*Table 1. PWR species and number of occurrences per species.*

| PWR                                 | Occurrences  |
|-------------------------------------|--------------|
| <i>Solanum acule</i>                | 2981         |
| <i>Solanum acroglasum</i>           | 43           |
| <i>Solanum acrosapicum</i>          | 78           |
| <i>Solanum agrimonifolium</i>       | 262          |
| <i>Solanum albicans</i>             | 309          |
| <i>Solanum albomaii</i>             | 25           |
| <i>Solanum andreaeum</i>            | 455          |
| <i>Solanum ayauchense</i>           | 10           |
| <i>Solanum berthaultii</i>          | 913          |
| <i>Solanum bolivense</i>            | 1802         |
| <i>Solanum bombycinum</i>           | 8            |
| <i>Solanum brevicaulis</i>          | 4679         |
| <i>Solanum buesii</i>               | 66           |
| <i>Solanum bulbocastanum</i>        | 851          |
| <i>Solanum burkartii</i>            | 35           |
| <i>Solanum cajamarquense</i>        | 83           |
| <i>Solanum candolleianum</i>        | 3269         |
| <i>Solanum canterense</i>           | 115          |
| <i>Solanum chacoense</i>            | 1976         |
| <i>Solanum chilliense</i>           | 16           |
| <i>Solanum chiquidenum</i>          | 259          |
| <i>Solanum chomatophilum</i>        | 918          |
| <i>Solanum clarum</i>               | 192          |
| <i>Solanum colombianum</i>          | 843          |
| <i>Solanum comersonii</i>           | 575          |
| <i>Solanum contumazaense</i>        | 19           |
| <i>Solanum demissum</i>             | 1631         |
| <i>Solanum flahaultii</i>           | 87           |
| <i>Solanum gandarillasii</i>        | 50           |
| <i>Solanum garcia-barrigae</i>      | 17           |
| <i>Solanum graefifrons</i>          | 18           |
| <i>Solanum guereiroense</i>         | 5            |
| <i>Solanum hastiforme</i>           | 49           |
| <i>Solanum hintanii</i>             | 30           |
| <i>Solanum hjertingii</i>           | 153          |
| <i>Solanum hugoii</i>               | 174          |
| <i>Solanum huancabambense</i>       | 57           |
| <i>Solanum inasicum</i>             | 11           |
| <i>Solanum infundibuliforme</i>     | 959          |
| <i>Solanum iopetalum</i>            | 641          |
| <i>Solanum iurtianum</i>            | 670          |
| <i>Solanum laxissimum</i>           | 138          |
| <i>Solanum lesteri</i>              | 21           |
| <i>Solanum limbanense</i>           | 64           |
| <i>Solanum longianicum</i>          | 471          |
| <i>Solanum magilla</i>              | 146          |
| <i>Solanum medians</i>              | 861          |
| <i>Solanum microdonum</i>           | 997          |
| <i>Solanum morelliforme</i>         | 311          |
| <i>Solanum multiinleruptum</i>      | 539          |
| <i>Solanum neocarde-nasii</i>       | 27           |
| <i>Solanum neocarsii</i>            | 82           |
| <i>Solanum neo-vilavii</i>          | 19           |
| <i>Solanum nubicola</i>             | 35           |
| <i>Solanum okadae</i>               | 155          |
| <i>Solanum olmoseense</i>           | 22           |
| <i>Solanum oxycarpum</i>            | 210          |
| <i>Solanum paucisectum</i>          | 76           |
| <i>Solanum pillahuatense</i>        | 16           |
| <i>Solanum piurae</i>               | 95           |
| <i>Solanum polyadenium</i>          | 253          |
| <i>Solanum raphanifolium</i>        | 682          |
| <i>Solanum rhomboidellacealatum</i> | 100          |
| <i>Solanum salianum</i>             | 13           |
| <i>Solanum schenkii</i>             | 110          |
| <i>Solanum sogorandinum</i>         | 159          |
| <i>Solanum stolarifolium</i>        | 4475         |
| <i>Solanum tarnii</i>               | 88           |
| <i>Solanum venturii</i>             | 116          |
| <i>Solanum vernei</i>               | 409          |
| <i>Solanum verrucosum</i>           | 994          |
| <i>Solanum violaceimarmoratum</i>   | 232          |
| <b>Total</b>                        | <b>37250</b> |

*Table 2. PCA Loadings and Correlations with BioClim Variables.*

| BioClim Variables |                                  | Loadings |        | Correlations |        |
|-------------------|----------------------------------|----------|--------|--------------|--------|
|                   |                                  | PC1      | PC2    | PC1          | PC2    |
| bio_01            | annual mean temperature          | -0.309   | 0.174  | -0.914       | 0.357  |
| bio_02            | mean diurnal range               | 0.045    | 0.303  | 0.134        | 0.622  |
| bio_03            | isothermality                    | -0.263   | 0.022  | -0.78        | 0.045  |
| bio_04            | temperature seasonality          | 0.291    | -0.019 | 0.861        | -0.039 |
| bio_05            | max temp of warmest month        | -0.177   | 0.297  | -0.523       | 0.61   |
| bio_06            | min temp of coldest month        | -0.321   | 0.079  | -0.951       | 0.163  |
| bio_07            | temperature annual range         | 0.288    | 0.074  | 0.853        | 0.152  |
| bio_08            | mean temp of wettest quarter     | -0.197   | 0.152  | -0.585       | 0.311  |
| bio_09            | mean temp of driest quarter      | -0.278   | 0.137  | -0.825       | 0.281  |
| bio_10            | mean temp of warmest quarter     | -0.215   | 0.242  | -0.638       | 0.496  |
| bio_11            | mean temp of coldest quarter     | -0.319   | 0.122  | -0.946       | 0.25   |
| bio_12            | annual precipitation             | -0.252   | -0.283 | -0.748       | -0.58  |
| bio_13            | precipitation of wettest month   | -0.25    | -0.092 | -0.74        | -0.19  |
| bio_14            | precipitation of driest month    | -0.101   | -0.394 | -0.298       | -0.808 |
| bio_15            | precipitation seasonality        | -0.07    | 0.328  | -0.208       | 0.674  |
| bio_16            | precipitation of wettest quarter | -0.255   | -0.118 | -0.755       | -0.242 |
| bio_17            | precipitation of driest quarter  | -0.11    | -0.396 | -0.324       | -0.813 |
| bio_18            | precipitation of warmest quarter | -0.152   | -0.261 | -0.449       | -0.536 |
| bio_19            | precipitation of coldest quarter | -0.16    | -0.267 | -0.475       | -0.549 |

**Table 3.** Top two species' PWRP values under SSP 4.5 in 2050 for each climate class. Green represents a change in the top two or a rank change in alternative SSP and year scenarios. The presence of these species indicate they may be the most suitable parents for crossing to potato to improve adaptation to future climates in the noted climate class.

| Koppen-Geiger Climate                       |                             | Species                        | Value |
|---|-----------------------------|--------------------------------|-------|
| Af  | Tropical Rainforest         | <i>Solanum colombianum</i>     | 0.250 |
|   |                             | <i>Solanum longiconicum</i>    | 0.234 |
| Am  | Tropical Monsoon            | <i>Solanum garcia-barrigae</i> | 0.417 |
|   |                             | <i>Solanum longiconicum</i>    | 0.361 |
| As  | Tropical Savanna Dry-Summer | <i>Solanum andreanum</i>       | 0.039 |
|   |                             | <i>Solanum bougasii</i>        | 0.034 |
| Aw  | Tropical Savanna Dry-Winter | <i>Solanum chillasense</i>     | 1.646 |
|   |                             | <i>Solanum neocardenasii</i>   | 0.501 |
| BSh   | Hot Semi-Arid               | <i>Solanum olmosense</i>       | 1.032 |
|   |                             | <i>Solanum paucisectum</i>     | 0.767 |
| BSk   | Cold Semi-Arid              | <i>Solanum gracilifrons</i>    | 1.705 |
|   |                             | <i>Solanum contumazense</i>    | 1.678 |
| BWh   | Hot Desert                  | <i>Solanum buancabambense</i>  | 0.184 |
|   |                             | <i>Solanum cajamarquense</i>   | 0.173 |
| BWk   | Cold Desert                 | <i>Solanum acroscopicum</i>    | 0.464 |
|   |                             | <i>Solanum medians</i>         | 0.175 |
| Cfa   | Humid Subtropical           | <i>Solanum comersonii</i>      | 0.798 |
|   |                             | <i>Solanum chacoense</i>       | 0.766 |
| Cfb   | Temperate oceanic           | <i>Solanum neocardenasii</i>   | 2.013 |
|   |                             | <i>Solanum pillahuatense</i>   | 1.836 |
| Cfc   | Subpolar oceanic            | <i>Solanum incasicum</i>       | 1.869 |
|   |                             | <i>Solanum buesii</i>          | 1.103 |
| Csa   | Hot-summer Mediterranean    | <i>Solanum stoloniferum</i>    | 0.070 |
|   |                             | <i>Solanum iobetalum</i>       | 0.008 |
| Csb   | Warm-summer Mediterranean   | <i>Solanum andreanum</i>       | 0.466 |
|   |                             | <i>Solanum colombianum</i>     | 0.168 |
| Cwa   | Monsoon humid subtropical   | <i>Solanum chacoense</i>       | 0.401 |
|   |                             | <i>Solanum bougasii</i>        | 0.305 |
| Cwb   | Subtropical highland        | <i>Solanum neorossii</i>       | 1.784 |
|   |                             | <i>Solanum gandarillasii</i>   | 1.540 |
| Cwc   | Cold subtropical highland   | <i>Solanum venturii</i>        | 0.106 |
|   |                             | <i>Solanum brevicaule</i>      | 0.057 |
| ET  | Polar tundra                | <i>Solanum neovavilovii</i>    | 1.780 |
|   |                             | <i>Solanum limbanense</i>      | 1.285 |
| Top-2 Change with Change in Scenario        |                             |                                |       |
| Top-2 Do Not Change with Change in Scenario |                             |                                |       |



**Table 4.** 80 Highest valued PWRP (SSP 8.5 in 2070). The table shows the highest scoring species by climate combinations for the worst-case scenario in 2070.

| Potato Wild Relative Species         | Köppen-Geiger Climate       | PWRP Value | Potato Wild Relative Species         | Köppen-Geiger Climate       | PWRP Value |
|--------------------------------------|-----------------------------|------------|--------------------------------------|-----------------------------|------------|
| <i>Solanum calambianum</i>           | Temperate oceanic           | 2.086      | <i>Solanum brevicornis</i>           | Subtropical highland        | 0.780      |
| <i>Solanum incaeanum</i>             | Subpolar oceanic            | 1.877      | <i>Solanum parvisectum</i>           | Hot Semi-Arid               | 0.769      |
| <i>Solanum pillabastense</i>         | Temperate oceanic           | 1.844      | <i>Solanum marulifolium</i>          | Subtropical highland        | 0.765      |
| <i>Solanum neorossii</i>             | Subtropical highland        | 1.784      | <i>Solanum parvisectum</i>           | Temperate oceanic           | 0.747      |
| <i>Solanum neorossii</i>             | Polar tundra                | 1.779      | <i>Solanum bulbocastanum</i>         | Subtropical highland        | 0.745      |
| <i>Solanum aculeense</i>             | Temperate oceanic           | 1.740      | <i>Solanum anitense</i>              | Cold Semi-Arid              | 0.732      |
| <i>Solanum alazanum</i>              | Temperate oceanic           | 1.706      | <i>Solanum anitense</i>              | Polar tundra                | 0.732      |
| <i>Solanum graciliflorum</i>         | Cold Semi-Arid              | 1.704      | <i>Solanum huancabambense</i>        | Hot Semi-Arid               | 0.702      |
| <i>Solanum cantuzogense</i>          | Cold Semi-Arid              | 1.677      | <i>Solanum lasiiforme</i>            | Cold Semi-Arid              | 0.681      |
| <i>Solanum nescariense</i>           | Temperate oceanic           | 1.668      | <i>Solanum medianum</i>              | Polar tundra                | 0.670      |
| <i>Solanum chilense</i>              | Tropical Savanna Dry-Winter | 1.663      | <i>Solanum cajamarquense</i>         | Temperate oceanic           | 0.635      |
| <i>Solanum pandanilloi</i>           | Subtropical highland        | 1.540      | <i>Solanum iopetalum</i>             | Subtropical highland        | 0.627      |
| <i>Solanum aycayhuam</i>             | Temperate oceanic           | 1.476      | <i>Solanum andeanum</i>              | Warm-summer Mediterranean   | 0.625      |
| <i>Solanum andeanum</i>              | Temperate oceanic           | 1.420      | <i>Solanum longiconium</i>           | Tropical Monsoon            | 0.601      |
| <i>Solanum albarozoi</i>             | Temperate oceanic           | 1.369      | <i>Solanum raphanifolium</i>         | Polar tundra                | 0.599      |
| <i>Solanum ventarii</i>              | Subtropical highland        | 1.324      | <i>Solanum raphanifolium</i>         | Temperate oceanic           | 0.592      |
| <i>Solanum burkartii</i>             | Subtropical highland        | 1.313      | <i>Solanum nudicola</i>              | Temperate oceanic           | 0.573      |
| <i>Solanum limbanense</i>            | Polar tundra                | 1.287      | <i>Solanum microdonum</i>            | Subtropical highland        | 0.562      |
| <i>Solanum huancabambense</i>        | Temperate oceanic           | 1.265      | <i>Solanum bambusinum</i>            | Polar tundra                | 0.557      |
| <i>Solanum acroglorum</i>            | Temperate oceanic           | 1.196      | <i>Solanum stoloniferum</i>          | Cold Semi-Arid              | 0.552      |
| <i>Solanum akaiabe</i>               | Subtropical highland        | 1.149      | <i>Solanum stoloniferum</i>          | Subtropical highland        | 0.534      |
| <i>Solanum agrimonifolium</i>        | Subtropical highland        | 1.130      | <i>Solanum rhomboidellanceolatum</i> | Temperate oceanic           | 0.522      |
| <i>Solanum huaczi</i>                | Subpolar oceanic            | 1.115      | <i>Solanum violaceo-marmoratum</i>   | Temperate oceanic           | 0.506      |
| <i>Solanum rhomboidellanceolatum</i> | Polar tundra                | 1.046      | <i>Solanum bougainii</i>             | Monsoon humid subtropical   | 0.499      |
| <i>Solanum olmaense</i>              | Hot Semi-Arid               | 1.037      | <i>Solanum chacoense</i>             | Monsoon humid subtropical   | 0.499      |
| <i>Solanum longiconium</i>           | Temperate oceanic           | 1.010      | <i>Solanum agrimonifolium</i>        | Tropical Savanna Dry-Winter | 0.484      |
| <i>Solanum cammerarii</i>            | Humid Subtropical           | 1.009      | <i>Solanum olmaense</i>              | Tropical Savanna Dry-Winter | 0.478      |
| <i>Solanum lezneri</i>               | Subtropical highland        | 0.994      | <i>Solanum marulifolium</i>          | Temperate oceanic           | 0.471      |
| <i>Solanum tami</i>                  | Temperate oceanic           | 0.994      | <i>Solanum limbanense</i>            | Temperate oceanic           | 0.467      |
| <i>Solanum lasiiforme</i>            | Temperate oceanic           | 0.984      | <i>Solanum acroscopicum</i>          | Cold Desert                 | 0.466      |
| <i>Solanum chacoense</i>             | Humid Subtropical           | 0.951      | <i>Solanum burkartii</i>             | Temperate oceanic           | 0.453      |
| <i>Solanum elaeagnifolium</i>        | Cold Semi-Arid              | 0.917      | <i>Solanum violaceo-marmoratum</i>   | Subpolar oceanic            | 0.443      |
| <i>Solanum cajamarquense</i>         | Cold Semi-Arid              | 0.877      | <i>Solanum chomatophyllum</i>        | Temperate oceanic           | 0.442      |
| <i>Solanum polydonum</i>             | Subtropical highland        | 0.835      | <i>Solanum hirtinifolium</i>         | Cold Semi-Arid              | 0.430      |
| <i>Solanum verticillatum</i>         | Subtropical highland        | 0.832      | <i>Solanum medianum</i>              | Cold Semi-Arid              | 0.428      |
| <i>Solanum flabauitii</i>            | Temperate oceanic           | 0.825      | <i>Solanum acule</i>                 | Subtropical highland        | 0.427      |
| <i>Solanum chacoense</i>             | Subtropical highland        | 0.817      | <i>Solanum garcia-barrigae</i>       | Tropical Monsoon            | 0.427      |
| <i>Solanum acroscopicum</i>          | Polar tundra                | 0.806      | <i>Solanum aycayhuam</i>             | Subtropical highland        | 0.422      |
| <i>Solanum huaczi</i>                | Subtropical highland        | 0.791      | <i>Solanum nescariense</i>           | Tropical Savanna Dry-Winter | 0.415      |
| <i>Solanum demissum</i>              | Subtropical highland        | 0.788      | <i>Solanum nescariense</i>           | Subtropical highland        | 0.415      |

**Table 5.** Volume overlap matrix in principal component space by discrete climate classes. This table can serve to identify discrete niches with similar volume to assist in species selection where the local production niche is not represented in Table 1.

|     | Af    | Am    | As   | Av    | Bsh  | BSk   | BWh  | BWk  | Ca    | Cb    | Cfc   | Csa   | Csb   | Csc   | Cwa   | Cwb   | Cwc  | Dfa  | Dfb   | Dfc   | Dfd  | Dsa  | Dsb  | Dsc  | Dsd  | Dwa  | Dwb  | Dwc  | Dwd  | EF    | ET    |       |      |
|-----|-------|-------|------|-------|------|-------|------|------|-------|-------|-------|-------|-------|-------|-------|-------|------|------|-------|-------|------|------|------|------|------|------|------|------|------|-------|-------|-------|------|
| Af  | 23.65 | 13.01 | 3.12 | 6.10  | 0.00 | 0.00  | 0.00 | 0.00 | 5.35  | 7.90  | 0.00  | 0.01  | 0.74  | 0.00  | 7.62  | 5.95  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  |      |
| Am  | 13.01 | 21.65 | 6.80 | 10.82 | 1.57 | 0.28  | 0.15 | 0.00 | 7.82  | 9.54  | 0.00  | 2.08  | 2.49  | 0.00  | 13.62 | 8.84  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  |      |
| As  | 3.12  | 6.80  | 8.44 | 7.91  | 2.57 | 0.58  | 0.45 | 0.00 | 6.12  | 6.86  | 0.00  | 2.89  | 2.90  | 0.00  | 8.07  | 6.48  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  | 0.00 |
| Av  | 6.10  | 10.82 | 7.91 | 13.56 | 3.09 | 0.88  | 0.63 | 0.00 | 6.98  | 8.24  | 0.00  | 3.27  | 2.91  | 0.00  | 12.16 | 8.47  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  | 0.00 |
| Bsh | 0.00  | 1.57  | 2.57 | 3.09  | 7.67 | 4.03  | 4.15 | 2.31 | 4.76  | 5.62  | 0.00  | 5.61  | 3.79  | 0.00  | 4.66  | 4.13  | 0.69 | 0.22 | 0.06  | 0.00  | 0.00 | 0.16 | 0.23 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  | 1.29 |
| BSk | 0.00  | 0.28  | 0.58 | 0.88  | 4.03 | 15.35 | 2.66 | 7.32 | 8.33  | 8.17  | 3.04  | 7.84  | 7.47  | 1.42  | 5.73  | 7.48  | 2.32 | 5.31 | 8.00  | 6.44  | 0.07 | 1.62 | 5.17 | 5.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  | 0.22 |
| BWh | 0.00  | 0.15  | 0.45 | 0.63  | 4.15 | 2.66  | 5.12 | 2.23 | 1.96  | 2.64  | 0.00  | 2.60  | 1.73  | 0.00  | 1.56  | 1.43  | 0.28 | 0.02 | 0.00  | 0.00  | 0.00 | 0.01 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  | 0.55 |
| BWk | 0.00  | 0.00  | 0.00 | 0.00  | 2.31 | 7.32  | 2.23 | 8.81 | 3.03  | 2.69  | 0.06  | 3.35  | 2.48  | 0.16  | 1.33  | 1.78  | 1.13 | 2.63 | 3.60  | 2.57  | 0.03 | 1.48 | 2.14 | 1.58 | 0.00 | 1.22 | 1.70 | 2.43 | 0.00 | 0.00  | 0.00  | 0.00  | 4.52 |
| Ca  | 5.35  | 7.82  | 6.12 | 6.98  | 4.76 | 8.33  | 1.96 | 3.03 | 2.65  | 2.96  | 9.64  | 9.58  | 17.06 | 3.61  | 14.88 | 19.70 | 2.32 | 4.57 | 6.18  | 3.06  | 0.00 | 1.40 | 3.44 | 1.65 | 0.00 | 2.88 | 2.09 | 1.18 | 0.00 | 0.00  | 0.00  | 8.37  |      |
| Cb  | 7.90  | 9.54  | 6.86 | 8.24  | 5.62 | 8.17  | 2.64 | 2.69 | 2.69  | 2.64  | 19.57 | 19.57 | 19.57 | 19.57 | 21.04 | 2.32  | 4.47 | 8.00 | 4.73  | 0.00  | 1.24 | 3.78 | 2.09 | 0.00 | 2.86 | 2.12 | 1.16 | 0.00 | 0.00 | 0.00  | 10.47 |       |      |
| Cfc | 0.00  | 0.00  | 0.00 | 0.00  | 3.04 | 0.00  | 0.06 | 0.06 | 9.64  | 19.57 | 23.96 | 2.57  | 8.70  | 5.32  | 3.59  | 7.78  | 1.13 | 2.98 | 7.09  | 4.43  | 0.00 | 0.20 | 2.31 | 1.86 | 0.00 | 2.10 | 1.60 | 0.66 | 0.00 | 0.00  | 0.01  | 8.28  |      |
| Csa | 0.01  | 2.08  | 2.89 | 3.27  | 5.61 | 7.84  | 2.60 | 3.35 | 9.58  | 9.91  | 2.57  | 10.65 | 8.01  | 1.01  | 8.38  | 8.31  | 2.06 | 3.17 | 2.91  | 1.11  | 0.00 | 1.48 | 2.32 | 0.43 | 0.00 | 2.19 | 0.97 | 0.55 | 0.00 | 0.00  | 0.00  | 5.04  |      |
| Csb | 0.74  | 2.49  | 2.90 | 2.91  | 3.79 | 7.47  | 1.73 | 2.48 | 17.06 | 16.84 | 8.70  | 8.01  | 17.11 | 3.27  | 10.12 | 14.22 | 2.30 | 4.03 | 5.36  | 2.41  | 0.00 | 0.93 | 2.75 | 1.29 | 0.00 | 2.68 | 1.77 | 0.93 | 0.00 | 0.00  | 0.00  | 7.46  |      |
| Csc | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 1.42  | 0.00 | 0.16 | 3.61  | 5.43  | 5.32  | 1.01  | 3.27  | 5.43  | 1.16  | 3.03  | 0.87 | 1.88 | 3.53  | 2.24  | 0.00 | 0.29 | 1.48 | 0.83 | 0.00 | 1.35 | 1.25 | 0.42 | 0.00 | 0.00  | 0.00  | 3.65  |      |
| Cwa | 7.62  | 13.62 | 8.07 | 12.16 | 4.66 | 5.73  | 1.56 | 1.33 | 14.88 | 16.17 | 3.59  | 8.38  | 10.12 | 1.16  | 22.26 | 16.35 | 1.87 | 2.51 | 2.38  | 0.70  | 0.00 | 0.52 | 1.43 | 0.31 | 0.00 | 1.96 | 0.71 | 0.23 | 0.00 | 0.00  | 0.00  | 4.41  |      |
| Cwb | 5.95  | 8.84  | 6.48 | 8.47  | 4.13 | 7.48  | 1.43 | 1.78 | 19.70 | 21.04 | 7.78  | 8.31  | 14.22 | 3.03  | 16.35 | 22.81 | 2.25 | 3.98 | 6.83  | 4.19  | 0.00 | 0.73 | 3.97 | 2.83 | 0.00 | 2.57 | 2.16 | 1.32 | 0.00 | 0.00  | 0.25  | 8.94  |      |
| Cwc | 0.00  | 0.00  | 0.00 | 0.00  | 0.69 | 2.32  | 0.28 | 1.13 | 2.32  | 2.32  | 1.13  | 2.06  | 2.30  | 0.87  | 1.87  | 2.25  | 2.32 | 1.75 | 1.56  | 0.71  | 0.00 | 0.70 | 1.60 | 0.48 | 0.00 | 1.12 | 0.63 | 0.40 | 0.00 | 0.00  | 0.00  | 2.31  |      |
| Dfa | 0.00  | 0.00  | 0.00 | 0.00  | 0.22 | 5.31  | 0.02 | 2.63 | 4.57  | 4.47  | 2.98  | 3.17  | 4.03  | 1.88  | 2.51  | 3.98  | 1.75 | 6.10 | 5.82  | 3.44  | 0.00 | 1.46 | 4.16 | 2.12 | 0.00 | 3.53 | 3.20 | 2.37 | 0.00 | 0.00  | 0.00  | 6.02  |      |
| Dfb | 0.00  | 0.00  | 0.00 | 0.00  | 0.06 | 8.00  | 0.00 | 3.60 | 6.18  | 8.00  | 7.09  | 2.91  | 5.26  | 3.53  | 2.38  | 6.83  | 1.56 | 5.82 | 14.29 | 10.57 | 0.00 | 1.36 | 5.88 | 6.55 | 0.00 | 3.52 | 4.60 | 4.92 | 0.00 | 0.00  | 0.00  | 13.97 |      |
| Dfc | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 6.44  | 0.00 | 2.57 | 3.06  | 4.73  | 4.43  | 1.11  | 2.41  | 2.24  | 0.70  | 4.19  | 0.71 | 3.44 | 10.57 | 16.60 | 1.83 | 0.57 | 4.76 | 9.25 | 0.00 | 2.27 | 4.47 | 5.71 | 0.61 | 4.52  | 16.57 |       |      |
| Dfd | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 0.07  | 0.00 | 0.03 | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00 | 0.00 | 0.81 | 0.00 | 0.00 | 0.00 | 0.33 | 0.77 | 0.56 | 2.33  |       |       |      |
| Dsa | 0.00  | 0.00  | 0.00 | 0.00  | 0.16 | 1.62  | 0.01 | 1.48 | 1.40  | 1.24  | 0.20  | 1.48  | 0.93  | 0.29  | 0.52  | 0.73  | 0.70 | 1.46 | 1.36  | 0.57  | 0.00 | 1.62 | 1.42 | 0.22 | 0.00 | 0.69 | 0.34 | 0.32 | 0.00 | 0.00  | 0.00  | 1.45  |      |
| Dsb | 0.00  | 0.00  | 0.00 | 0.00  | 0.23 | 5.17  | 0.02 | 2.14 | 3.44  | 3.78  | 2.31  | 2.32  | 2.75  | 1.48  | 1.43  | 3.97  | 1.60 | 4.16 | 5.88  | 4.76  | 0.00 | 1.42 | 6.08 | 3.87 | 0.00 | 2.65 | 3.36 | 2.79 | 0.00 | 0.26  | 6.05  |       |      |
| Dsc | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 5.07  | 0.00 | 1.58 | 1.65  | 2.09  | 1.86  | 0.43  | 1.29  | 0.83  | 0.31  | 2.83  | 0.48 | 2.12 | 6.55  | 9.25  | 0.81 | 0.22 | 3.87 | 9.25 | 0.00 | 1.59 | 3.41 | 4.91 | 0.43 | 2.38  | 9.25  |       |      |
| Dsd | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 0.00  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00  | 0.00  |       |      |
| Dwa | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 3.24  | 0.00 | 1.22 | 2.88  | 2.86  | 2.10  | 2.19  | 2.68  | 1.35  | 1.96  | 2.57  | 1.12 | 3.53 | 3.52  | 2.27  | 0.00 | 0.69 | 2.65 | 1.59 | 0.00 | 3.57 | 2.18 | 1.67 | 0.00 | 0.00  | 0.00  | 3.57  |      |
| Dwb | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 4.38  | 0.00 | 1.70 | 2.09  | 2.12  | 1.60  | 0.97  | 1.77  | 1.25  | 0.71  | 2.16  | 0.63 | 3.20 | 4.60  | 4.47  | 0.00 | 0.34 | 3.36 | 3.41 | 0.00 | 2.18 | 4.60 | 3.60 | 0.00 | 0.00  | 0.00  | 4.60  |      |
| Dwc | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 5.47  | 0.00 | 2.43 | 1.18  | 1.16  | 0.66  | 0.55  | 0.93  | 0.42  | 0.23  | 1.32  | 0.40 | 2.57 | 4.92  | 5.71  | 0.33 | 0.32 | 2.79 | 4.91 | 0.00 | 1.67 | 3.60 | 5.84 | 0.12 | 0.23  | 5.80  |       |      |
| Dwd | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 0.01  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00  | 0.00 | 0.00 | 0.00  | 0.00  | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.12 | 0.80 | 0.00 | 0.75  |       |       |      |
| EF  | 0.00  | 0.00  | 0.00 | 0.00  | 0.00 | 0.22  | 0.00 | 0.00 | 0.00  | 0.00  | 0.01  | 0.00  | 0.00  | 0.00  | 0.00  | 0.25  | 0.00 | 0.00 | 1.14  | 4.52  | 0.56 | 0.00 | 0.26 | 2.28 | 0.00 | 0.00 | 0.00 | 0.23 | 0.00 | 14.82 | 8.21  |       |      |
| ET  | 0.00  | 0.00  | 0.00 | 0.00  | 1.29 | 10.41 | 0.55 | 4.52 | 8.37  | 10.47 | 8.28  | 5.04  | 7.46  | 3.65  | 4.41  | 8.94  | 2.31 | 6.02 | 13.97 | 16.57 | 2.33 | 1.43 | 6.05 | 9.25 | 0.00 | 3.57 | 4.60 | 5.80 | 0.75 | 8.21  | 30.58 |       |      |

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## Additional Work

### *HLARC-HSPA Sustainable Agriculture Fellowship*

1. Germplasm maintenance of Stevia, Papaya, Sugarcane, Koa, Sandalwood, Coffee, Cacao
2. Lead of Stevia breeding and improvement
  - a. Polycross of Generation 1 (F1) and Parental Lines for creation of Generation 2 (F2)
  - b. Augmented Randomized Complete Block Design and Analysis of Parental Family Lines, Generation 1, and Generation 2.
    - i. Two environments, about 350 varieties per environment, 10 blocks per environment, 35 plots per block
  - c. Polycross of Elite Varieties found in Item 2b for creation of Generation 3 (F3)
    - i. Beginning stages of Controlled Environment Trials on Phenotypes Photoperiod Inducing Flowering and Total Steviol Glycosides Content from Generation 3
3. Heritability Analysis of Steviol Glycosides in Stevia family lines
4. Propagation assistance
  - a. Papaya – Clonal propagation
  - b. Koa – Air-layer propagation
  - c. Sandalwood – Air-layer propagation

### *Additional Publications*

1. Pironon, S., Borrell, J.S., Ondo, I., Douglas, R., Phillips, C., Khoury, C.K., Kantar, M.B., **Fumia, N.**, Soto Gomez, M., Viruel, J., Govaerts, R., Forest, F., Antonelli, A. (2020). Toward Unifying Global Hotspots of Wild and Domesticated Biodiversity. *Plants*, 9, 1128.
2. Del Valle Echevarria, AR, **Fumia, N.**, Gore, MA, Kantar, MB. Domestication and Plant Breeding. (*in review Plant Breeding Reviews*)

### *Lectures*

1. TPSS 300 (Spring 2020): Field and Greenhouse Crop Production

### *Presentations*

1. EECB Evoluncheon Feedback Workshop (Spring 2021): Climate Forecasting with Principal Component Analysis
2. TPSS Seminar (Spring 2021): Exploring the resilience and optimizing the uses of potato wild relative species (*Solanum* Section *Petota*) in a changing climate.

### *Additional Training*

1. Tucson Plant Breeding Institute: Module 1 (Introduction to Plant Quantitative Genetics) & Module 2 (Advanced Statistical Plant Breeding); Dr. Bruce Walsh, Dr. Mike Gore, Dr. Lucia Gutierrez; University of Arizona; January 6-10, 2020