Domestication, invasion, and ethnobotany of *Brassica rapa*

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Dissertation overview and chapter summaries

The species *Brassica rapa* is native to Eurasia and Africa and consists of morphologically diverse crops (e.g., turnips, napa cabbage, pak choi, oilseeds) and spontaneously occurring forms (field mustard). Despite the economic importance of *B. rapa* worldwide, details surrounding its wild forms, domestication, and spread as an invasive species are unclear, limiting the ability of breeders to adapt crops to new stresses and hampering control of weedy forms. Weedy field mustard in Latin America has been widely adopted by Indigenous peoples as a food and medicine and in some cases, cultures have begun to intensively collect and sow seeds in dedicated plots. This presents a study system to understand how ethnobotanical knowledge of newly encountered plants is formed to study domestication as a contemporary process. We combined ethnographic interviews, genotyping-by-sequencing data, niche modeling, and a common garden experiment to investigate the following overarching questions: 1) are spontaneously occurring populations of *B. rapa* truly wild or feral escapes? 2) what is the domestication history of *B. rapa*? *3)* what are the origins of invasive *B. rapa*? 4) how does Indigenous use, management, and preference for *B. rapa* vary throughout the Americas and 5) what are the evolutionary consequences of *B. rapa* management by Indigenous farmers in northwestern Mexico?

In **chapter one,** we reviewed research on wild and weedy forms of *B. rapa*, highlighted gaps in knowledge, and suggested future courses of study. We identified the following priorities in *B. rapa* research: revision of infraspecific taxonomy, correction of mislabeled germplasm in seed banks, clarification of wild or feral status of spontaneously occurring populations, and inclusion of wild forms in domestication research.

In **chapter two,** we investigated the domestication history of *B. rapa* crops and wild or feral nature of spontaneously occurring populations using genotyping-by-sequencing and species distribution modeling. We analyzed genetic structure, diversity, and demography of the largest-to-date diversity panel of *B. rapa* crops and weedy forms. These analyses suggest that spontaneously occurring populations from the Caucasus were from truly wild populations, while those from other parts of Europe had a feral origin from European crops. Our findings also supported turnips as the first domesticated *B. rapa* crop, with parallel selection on turnips in Europe and East Asia resulting in oilseeds and leaf crops. Our species distribution model for mid-Holocene Eurasia suggested a nearly contiguous potential distribution of wild *B. rapa* from Iberia to China.

In **chapter three**, we investigated the feral origins of *B. rapa* in Europe and reconstructed the spread of weedy *B. rapa* into the Americas with genotyping-by-sequencing and niche modeling. Our analyses of genetic structure and diversity suggested that feral *B. rapa* originated from European crops that experienced introgression from sympatric wild populations. We also found evidence for separate origins of invasive *B. rapa* introduced into Canada and Latin America. Canadian weeds were closely associated with northern European turnips, while Latin American weeds were more closely associated with Mediterranean crops. We did not detect a substantial reduction in diversity from the native range to the introduced range, but the niches occupied in Europe and Latin America differed.

In **chapter four**, we compared use, management, and preferences for *B. rapa* across ethnic groups in Latin America. We conducted semi-structured interviews and structured surveys with eight ethnic groups across Mexico and compared the results qualitatively and quantitatively. We found that use and management of *B. rapa* was patterned both by geographic proximity and linguistic affiliation between groups. We documented several cases in which weedy *B. rapa* was encouraged through transplanting, sowing, and sparing from weeding. In many areas, there was evidence of declining cultivation and use of *B. rapa* due to changing livelihoods and availability of processed foods.

In **chapter five**, we investigated the genetic and phenotypic consequences of weedy *B. rapa* cultivation by Rarámuri farmers in Chihuahua, Mexico. We collected field mustard samples from 13 populations in 9 Rarámuri communities and conducted a common garden experiment and genotyping-by-sequencing-based population genetic analyses. We found significant differences in flowering time between managed and unmanaged populations and genetic differentiation of two managed populations from unmanaged populations in the same communities.

Overall, our research contributes to knowledge of wild and crop genetic resources in a globally distributed multi-purpose crop species and clarifies the domestication, feralization, invasion, recent adoption, and potential ongoing redomestication of *B. rapa*. These findings provide the groundwork for future studies of the genetic basis of domestication and weediness in a species with the experimental benefits of a short life-cycle, sequenced genome, and close relationship to the model organism for plant genetics *Arabidopsis thaliana*.

Contents

Contributions of collaborators

Vice chair: Donald M. Waller

Eve Emshwiller contributed to planning each project, obtaining funding, and providing advice on writing each for the chapters.

Chapter 1: Barriers and prospects for wild crop relative research in *Brassica rapa*

Kevin Bird, Gert Poulsen, and Chris Pires provided consultation and feedback on content.

Chapter 2: Domestication history and wild forms of *Brassica rapa* clarified through Genotyping-By-Sequencing

Aaron Ragsdale assisted in optimizing parameters and creating the demographic model. Xinshuai Qi, Kevin Bird, and Chris Pires, contributed suggestions and technical support regarding the analyses. Pablo Velasco provided seeds and background information regarding Spanish turnips and Spanish grelos.

Chapter 4: Adopting and adapting: use and management of invasive field mustard (*Brassica rapa*) in Mexico

Antonio Eloy Arce provided support in the field when working with the communities of San Felipe del Progreso and Río Hoyo Buenavista. Heike Vibrans provided fieldwork support in Soledad Atzompa. Robert Bye provided fieldwork support in Soledad Atzompa and Rarámuri communities in Chihuahua.

Chapter 5: Genetic and phenotypic consequences of Indigenous management of feral *Brassica rapa* in Mexico

Robert Bye provided fieldwork support with Rarámuri communities in Chihuahua.

Chapter 1

Barriers and prospects for wild crop relative research in Brassica rapa

Alex C. McAlvay, Kevin Bird, Gert Poulsen, Chris Pires, Eve Emshwiller

Abstract

Wild relatives of crop plants provide information about crop domestication history and can contribute genetic material for breeding resilient crops. Wild forms of the multipurpose crop species *Brassica rapa* (pak choi, napa cabbage, turnips, turnip rape, sarson) are poorly characterized, compromising our understanding of the origins of domesticated forms and our ability to breed crops that are resilient to new biotic and abiotic challenges. We reviewed previous research on spontaneously occurring forms of *B. rapa* and highlighted gaps in current knowledge on the subject. It is not clear whether spontaneously occurring populations are truly wild or feral escapes from domesticated crops. Past research has been impeded by taxonomic confusion, limited collections of spontaneously occurring forms, and mislabeling in germplasm banks. This has resulted in low sampling of potentially wild forms in genetic studies and ultimately a lack of clarity surrounding the domestication origins and genetic resources of the species. We call for increased collection of *B. rapa* in its putative native range, infraspecific taxonomic revision, validation of germplasm in collections, and increased sampling of wild and/or feral forms in genetic studies. Additionally, we propose *B. rapa* as a potential model organism for studying domestication, dedomestication, and invasion.

Keywords: Brassicaceae, *Brassica rapa*, crop wild relatives, genetic resources,

Crop wild relatives, domestication, and genetic resources

Understanding the process of domestication provides insight into the nature of both contemporary crop genetic resources (Zeder, 2015) and evolutionary processes in general (e.g., Darwin, 1868; Andersson and Georges, 2004; Ross-Ibarra et al., 2007; Purugganan & Fuller 2009; Meyer and Purugganan, 2013; Olsen & Wendel 2013). Crop wild relatives are important resources for clarifying the origins of domesticated plants (Smýkal et al., 2011; Meyer et al., 2012). The distribution and genetic relationships of wild crop relatives can provide insights into the location(s) of domestication (Matsuoka et al., 2002), number of domestication events (Koenig and Gepts, 1989; Matsuoka et al., 2002; Guo et al., 2010), timing of domestication (Matsuoka et al., 2002), and the presence of genetic bottlenecks (Myles et al., 2011). Genetic analyses involving wild crop relatives can also help disentangle complex scenarios like the secondary contributions of wild relatives to domesticated species through introgression (Cornille et al., 2012) or wild-weedy-domesticated plant complexes (Zizumbo-Villarreal et al., 2005).

Various pools of diversity will be important in the future to face pests, climate change, environmental degradation, and other breeding challenges (Xiao et al., 1996; Guarino and Lobell 2011; McCouch et al., 2013). Domestication has led to major bottlenecks in genetic diversity (Tanksley and McCouch, 1997; Feuillet et al., 2008; Olsen and Gross 2008) which limits the diversity that can be used in breeding efforts. Wild relatives of crop plants have proved useful in plant breeding for resistance to biotic and abiotic stresses (Flis et al., 2005; Hajjar and Hodgkin, 2007; Honnay et al., 2012; Dempewolf et al., 2014) and provide an important resource for food security moving forward (Maxted et al., 2008; Jansky et al., 2013; Brozynska et al., 2016). Unfortunately, wild crop relatives are increasingly threatened by land use change, invasive species, and climate change (Jarvis et al., 2008; Maxted et al., 2012; Brummitt et al., 2015), and only represent a small portion of ex-situ genebank collections (Castaneda-Alvarez et al., 2016). Increased characterization and conservation of these resources would benefit long term food security (Meilleur and Hodgkin, 2004; Maxted and Kell, 2009; Iriondo et al., 2011).

Research on crop wild relatives has focused on cereals and legumes, leaving many wild relatives of other crops unidentified, under-collected, and/or underprotected (FAO, 2010). The genus *Brassica* includes numerous multicrop species, such as *B. oleracea* (cauliflower, broccoli, cabbage), *B. napus* (rutabaga, rapeseed), *B. rapa* (napa cabbage, pak choi, turnips), and various mustard crops (*B. nigra, B. juncea, and B. abyssinica*) which collectively valued around 14 billion dollars in 2014 (FAOSTAT). The European Cooperative Programme for Plant Genetic Resources and independent researchers have made progress to improve collections, identification, and conservation of these wild relatives, but much is still unclear (Andersen et al., 2009; Christensen et al., 2011; Branca et al., 2012; Haro-Bailón 2013; Branca et al., 2016).

Knowledge gaps and prospects in the study of wild *Brassica rapa*

Little is known about the wild forms of the multipurpose crop species (*Brassica rapa* L.). This species includes economically important crops such as turnips, leafy forms like pak choi, napa cabbage, mizuna, tatsoi, rapini, and choy sum as well as oilseed forms like turnip rape and sarsons (Gómez-Campo and Prakash, 1999; Purugganan *et al.* 2000; Zhao et al., 2005; Warwick et al., 2008; Prakash et al. 2009, 2011; Guo et al., 2014; see McAlvay, Chapter 2, Table 1). In addition to its value as a crop, *B. rapa* is a valuable source of alleles of agronomic interest for other *Brassica*, including the allotetraploids *B. napus* (rutabagas, leafy greens, and rapeseed) and *B. juncea* (leaf mustard and oilseeds) for which *B. rapa* is a genome donor (Qian et al., 2006; Mei et al., 2011) and which have undergone diversity bottlenecks from polyploidization (Cowling 2007).

In addition to crop forms, *B. rapa* also occurs spontaneously on roadsides, waste areas, farmlands, and riversides in temperate areas worldwide (Wilkinson et al. 2003; Hall et al., 2005; Andersen et al., 2009). These spontaneous forms, often called field mustard or birdsrape mustard, are an important study system for understanding the feasibility of transgene introgression from crops to wild congeners (Halfhill et al., 2004; Jørgensen and Andersen 1994; Bing et al., 1996; Landbo et al., 1996; Scott et al., 1999; Warwick et al., 2003; Steward et al., 2003; Chèvre 2004; Warwick et al., 2008; Andersen et al., 2009; Ellstrand, 2003). Field mustard has the potential to be a model study system for domestication, ferality, and invasion with its well annotated reference genome (Wang et al., 2011), close relationship to the model species for plant genetics, *Arabidopsis thaliana* (Paterson et al., 2001, Yang et al., 2005), and rapid life-cycle (Williams and Hill, 1986). We review the following, gaps, barriers, and prospects in *B. rapa* wild relative research: 1) taxonomic issues, 2) mislabelled germplasm, 3) differentiation of feral and wild populations, 4) conservation and collection of wild relatives, 5) origins of invasive populations, 6) omission of wild relatives from domestication research, and 7) ethnobotany of invasive populations.

Taxonomic issues—The infraspecific taxonomy of *Brassica* species has long been problematic for researchers (Robellen et al., 1989; Kalia and Gupta, 1997; Gupta and Pratap 2007). Shortcomings in the naming system of *B. rapa* have been revealed by numerous genetic studies which show a lack of monophyly in the oilseed subspecies ssp. *trilocularis*, ssp. *dichotoma*, and ssp. *oleifera* (Bird et al., 2017; Qi et al., 2017) and turnips (ssp. *rapa*) (Cheng et al., 2016; Bird et al., 2017). Furthermore, some leafy Mediterranean crops like rapini are classified as the same subspecies (ssp. *sylvestris*) as relatively distantly related spontaneous forms of *B. rapa.* Germplasm banks often employ different infraspecific taxonomic systems from each other and even within the same collection. For example, the system of Prakash and Hinata (1980) is still commonly used even though the more recent treatment of Diederichsen (2001) is widely accepted. The older name for *Brassica rapa—Brassica campestris L.*—can also still be found in many collections, making it difficult for researchers to find certain accessions unless searching for all synonyms. These issues have the potential to impede communication between researchers and germplasm banks. A new infraspecific taxonomy of *B. rapa* would contribute to more accurate domestication research and more effective breeding programs. A recent revision of infraspecific taxonomy in another crop species, *Daucus carota,* integrating morphogical and genetic data (Arbizu et al., 2016) provides a blueprint for an analogous project in *B. rapa*.

Mislabelled germplasm—In addition to taxonomic issues, mislabelling of germplasm accessions in global collections is common in the *Brassica* genus (Maggioni et al., 2013; Poulsen et al., 2013). These misidentifications can interfere with breeding efforts (Crouch et al. 1995) and conclusions about domestication origins. For example, *B. rapa* and *B. napus* are often confused with each other due to overlap in numerous several morphological characters (Luijten and J. de Jong, 2010). Wild *B. rapa* is characterized variously as *B. rapa* ssp. *sylvestris, B. rapa* ssp. *campestris* (a no longer accepted name), or as *B. rapa* ssp. *oleifera* (pers. observation). Due to germplasm labeling issues, a recent RNA-sequencing study by Qi et al. (2017) conflated Italian rapini (ssp. *sylvestris* L. Janch. var. *esculenta* Hort) and field mustard (ssp. *sylvestris* (L.) Janch), leading to misleading results. Accession details in the USDA database suggest that the actual rapini in the dataset were categorized as ssp. *oleifera* in the USDA collection, leading to further confusion. Some progress has been made to remove duplicates in germplasm databases (Report of a Working Group on *Brassica*, 2010) and identify unlabelled accessions (Artemyeva, 2013), but further efforts to comprehensively characterize current collections in seed banks worldwide would greatly facilitate research on *B. rapa*.

Feral and wild status unclear—Spontaneously occurring forms of crop species can be truly wild or derived from crops that have escaped cultivation and persist as feral populations (Gressel et al., 2005). In some crop species, spontaneous forms that were thought to be wild were later revealed to be escaped domesticates (Mithen & Kibblewhite, 1993; Vaillancourt et al., 1993). Even though feral populations of crop species have been leveraged in studies of local adapation and breeding potential (Li et al., 2017), they are not expected to harbor as much diversity as truly wild populations due to diversity bottlenecks from domestication and escape (Hall et al., 2005).

It is unclear whether many known weedy *B. rapa* populations are wild or feral (Crouch et al., 1995; Andersen et al., 2009), compromising breeding, conservation, and domestication research. Some researchers assert that truly wild *Brassica rapa* may be entirely extinct, with extant spontaneous populations all being feral (Ignatov et al., 1999), while others (e.g., Guo et al., 2014) assume that all spontaneous populations are wild. Andersen et al. (2009) attempted to distinguish between wild and feral populations in northern Europe using inter-simple sequence repeat markers and found that the spontaneously occurring populations were not closely related to escaped local cultivars, suggesting a wild or non-local feral origin. Population genomic studies with broad geographic sampling of spontaneous and cultivated *B. rapa* would help to clarify which populations are wild and which are feral. If feral populations are identified, further work to identify their origins, the genetic basis of weediness, and local adaptations could be carried out as has been done in weedy rice (Qiu et al. 2017), sea beet (Sukopp et al., 2005), and foxtail millet (Burger and Ellstrand, 2005). Few well characterized examples of ferality are known (Ellstrand et al., 2010), and field mustard's close relationship to *Arabidopsis* (Paterson et al., 2001, Yang et al., 2005) and well annotated genome (Wang et al., 2011) make it a potentially useful model system for understanding this phenomenon.

***Spontaneous populations threatened and access to new collections difficult*—**Many crop wild relatives are likely threatened by climate change (Jarvis et al., 2008; Ford-Lloyd et al., 2011) and other factors (Maxted et al., 2012). Wild *B. rapa* resources are likely declining and may be facing local extinction in parts of the native range (ECPGR *Brassica* Working Group, EU GEN RES 109-112), as they tend to grow in intensively managed agricultural lands where herbicide use may be prevalent, and in wetland areas that are often threatened habitats (Gressel et al., 2005). The loss of these wild resources would reduce our ability to breed resilient germplasm in response to new breeding challenges. The ECPGR *Brassica* Working Group has made progress toward both in-situ and ex-situ conservation of wild *Brassica*, but wild accessions are still underrepresented in collections (Maggioni and Lipman, 2010). Only 14 of 3769 (0.37%) of the *B. rapa* accessions in the European *Brassica* database are categorized as wild, natural, semi-natural, or weedy (http://ecpgr.cgn.wur.nl/Brasedb; Accessed 1/2/2018). New collections of spontaneous *B. rapa* could be challenging to obtain because of an unclear native range (Guo et al., 2014), limited funding for new collecting projects, permitting issues, and political instability in parts of the putative center of domestication. While recent initiatives to integrate germplasm collections into agglomerative databases like Eurisco and SINGER, a single comprehensive resource does not yet exist. A comprehensive assessment of spontaneous *Brassica rapa* genetic resources would be an important step for further conservation. This could take place through gap analysis, a technique adopted from conservation biology to compare the characteristics of a conservation target with current conservation strategies in place and identify deficiencies in current *in situ* and *ex situ* conservation efforts (Maxted et al., 2008; Ramírez-Villegas et al., 2010; Parra-Quijano et al., 2011; Castañeda-Álvarez et al. 2016). Gap analysis has been conducted with wild *Brassica* relatives such as *B. incana* and *B. montana* in Italy (Landucci et al., 2014), but not in *B. rapa*. Implimentation of optimized collecting design would help conserve germplasm from the breadth of the species' ecogeographical range (Parra-Quijano et al. 2012).

***Lack of research on invasive populations*—**Invasive species threaten local ecosystems, biodiversity, and agricultural production (Richardson and Pyšek, 2006; Prentis et al., 2007, Pyšek et al. 2012; Pyšek and Richardson 2011; Vilà et al. 2011). Reconstructing the route(s) and details of biological invasion provides important information for the control of invasive species (Garcia-Rossi et al., 2003; Muller-Scharer et al., 2004; Goolsby et al., 2006; Zalucki et al., 2007), provides general insights about how species colonize new areas, and an opportunity to study rapid local adaptation (Sax et al. 2007; Dlugosch and Parker, 2008). Weedy field mustard is regulated as a noxious weed in 11 U.S. states (MDA, 2011; Parker, 1972) and recognized as an invasive plant by the Mexican government (Vibrans, 2002; Comité Asesor Nacional sobre Especies Invasoras, 2010). Population genetic studies clarifying the genetic diversity, admixture, and source population(s) of the invading populations would enhance our understanding and management of field mustard. The short generation time, sequenced genome, and broad range across environmental gradients make invasive *B. rapa* a potentially powerful study system for understanding rapid evolution of introduced species.

***Omission of wild <u>Brassica</u> <u>rapa</u> from domestication research*—**The domestication of *B. rapa* remains opaque partially due to low sampling of wild *B. rapa* in genetic studies. Recent work on used a variety of genomic approaches and crop samples to provide new insights into the complexity of *Brassica* domestication. For example, microsatellites have helped identify western Eurasia or North Africa as a potential center of origin (Guo et al., 2014), demography reconstruction from RNA-seq data showed parallels between domestication events and historical written records (Qi et al., 2017), and whole genome resequencing and genotyping-by-sequencing datasets have clarified the relationships between various crop subspecies (Cheng et al. 2016, Bird et al., 2017). Insights have, however, been limited by low sampling of spontaneous forms (Table 1). Many of the accessions included in these studies were from the invaded range in the Americas. Andersen et al. (2009) included many wild collections in the putative native range, but not a broad sampling of domesticated individuals to compare them to. While many researchers place the center of domestication in Central Asia or Southwest Asia and some suggest a separate center in East Asia, wild forms in these areas are not available in major germplasm databases (e.g., Eurisco [accessed Dec. 5, 2017] or USDA GRIN [accessed Dec. 5, 2017]). Increased collection and sequencing of spontaneous forms and localized crop varieties in putative centers of origins would aid in disentangling the origins of domestication in *B. rapa*. This sampling combined with emerging demographic modeling approaches would allow researchers to explicitly address uncertainties about the origins of domestication such as the role of hybridization between crops and wild relatives, adaptation of domesticates to anthropogenic environments, and rates of domestication (Gerbault et al., 2014).

Table 1. Sampling of spontaneously occurring *Brassica rapa* included in recent studies of *B. rapa* domestication.

Technique	Study	# spontaneously occurring samples included
Microsatellites	Guo et al., 2014	7
RNA-sequencing	Qi et al., 2017	5
Genotyping-by-sequencing	Bird et al., 2016	5

Ethnobotany and potential ongoing domestication of weedy field mustard— Following the introduction of weedy *B. rapa* into the Americas, field mustard has been adopted and extensively used as food, medicine, and fodder by different cultures ranging from northwestern Mexico to Patagonia (e.g., Gade, 1972; Berlin et al., 1974; Bye, 1979; Ladio, 2001; Vieyra-Odilon and Vibrans, 2001). Several communities throughout Latin America have begun to actively encourage field mustard by sowing seeds in garden plots or sparing it when weeding their gardens (Gade, 1972; Bye, 1979; Vieyra-Odilon and Vibrans, 2001). There is a risk of conflicts in the future between individuals who eat and encourage this invasive plant and conservation organizations or farmers who would like to reduce its prevalence. The sowing of weedy *B. rapa* seeds by smale-scale farmers also provides a rare opportunity to directly study the cultural, ecological, and genetic context of domestication as it occurs. Most crops were domesticated thousands of years ago (Larson et al., 2014), making certain aspects of domestication difficult to study. In Latin America, several cases of ongoing domestication have provided insights into the process (Casas et al., 2007; Elias et al., 2007; Hughes et al., 2007; Blanckaert, 2011). Daniel Gade (1972), working in Peru, and Robert Bye (1979), working in Mexico, each suggested that weedy field mustard in Latin America might be under a domestication-like process due to management by Indigenous farmers.

Future directions

The identification, collection, characterization, and accessibility of spontaneous forms of *B. rapa* represents a research bottleneck, which precludes progress in understanding the process of domestication and invasion biology of this species. We suggest that future research should include the following steps: 1) taxonomic recircumscription of *B. rapa* subspecies, 2) correction of mislabelled germplasm in seed banks and databases, 3) genetic studies incorporating a broad sampling of spontaneously occurring populations and crop subspecies to clarify the wild/feral nature of populations, domestication history, and invasion biology of *B. rapa*, 4) species distribution modeling to aid collecting and conservation of wild *B. rapa*, 5) ethnobotanical studies of *B. rapa* in Latin America and elsewhere, and 6) effective communication of the importance of wild *B. rapa* to governmental bodies, farmers, and conservation organizations.

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Chapter 2

Domestication history and wild forms of *Brassica rapa* clarified through Genotyping-By-Sequencing.

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Abstract

The study of domestication contributes to our knowledge of artificial selection and crop genetic resources. Human selection has shaped wild field mustard (*Brassica rapa*) into diverse turnip, leafy (e.g pak choi, napa cabbage, rapini), and oilseed (e.g., sarsons, turnip rape) crops. Despite the economic importance of *B. rapa* crops worldwide, the nature of wild forms, center(s) of domestication, and historical spread are unclear, jeopardizing the ongoing resilience of *B. rapa* crop resources. To address this knowledge gap, we used genomic data from genotyping-by-sequencing to investigate genetic diversity, structure, and demography in the largest diversity panel of domesticated and spontaneously occurring *B. rapa* to date. We also constructed a species distribution model for wild *B. rapa* during the mid-Holocene, when domestication is thought to have occurred. Spontaneously occurring samples from the Caucasus had the highest nucleotide diversity and emerged as sister to all other *B. rapa* samples in our tree-based analyses, while weedy samples from Europe had lower diversity and were affiliated with European turnip crops. These results suggest that spontaneously occurring *B. rapa* in the Caucasus are truly wild, while those occurring in the Americas and much of Europe are feral. Clustering and tree-based analyses suggested that turnips were the first crop type domesticated with subsequent parallel selection for leafy and oilseed types in East Asia and Europe. These findings clarify the domestication history and nature of wild crop genetic resources for *B. rapa* which will be important for the conservation of crop wild relatives and understanding the complex process of domestication.

Keywords: Domestication, artificial selection, *Brassica rapa*, genotyping-by-sequencing

Introduction

Domestication is a process of adaptation to agro-ecological niches and human preferences (Larson et al., 2014) and is driven by a complex mix of ecological, biological, and cultural factors (Price et al., 2011; Gepts et al., 2012). The study of domestication provides insight into the nature of contemporary crop genetic resources (Zeder, 2015; Gepts et al., 2012) and evolutionary processes in general (Darwin, 1868; Andersson and Georges, 2004; Ross-Ibarra et al., 2007; Purugganan and Fuller 2009; Meyer and Purugganan, 2013; Fuller et al., 2014; Olsen & Wendel 2013).

The morphologically diverse crops in the genus *Brassica* (e.g., broccoli, cabbage, pak choi, and canola) provide powerful study systems to understand domestication and artificial selection (Gómez-Campo and Prakash, 1999; Zhao et al., 2005; Guo et al., 2014; Bird et al., 2017; Qi et al., 2017). Crops in the genus *Brassica* are also nutritionally and economically important worldwide, in total valuing around 14 billion dollars in 2014 (FAOSTAT). One major crop species is *Brassica rapa* L. (Brassicaceae: $2n = 20$), which includes diverse crop forms such as turnips, leafy crops like pak choi, napa cabbage, mizuna, tatsoi, rapini, grelos, and choy sum as well as oilseed crops like turnip rape and sarsons (Table 1; Gómez-Campo and Prakash, 1999; Zhao et al., 2005; Warwick et al., 2008; Guo et al., 2014; Purugganan et al. 2000; Prakash et al. 2009, 2011).

Table 1. Infraspecific taxonomy of *Brassica rapa* based on the system proposed by Diederichsen (2001). S/C Asia indicates South and Central Asia, including India, Pakistan, and Afghanistan.

Geography	**Common name**	**Latin name**	**Plant organ used**
S/C Asia	Yellow sarson	subsp. *trilocularis* (Roxb.) Hanelt	Seeds/leaves
S/C Asia	Toria/Brown sarson	subsp. *dichotoma* (Roxb.) Hanelt	Seeds/leaves
E. Asia	Komatsuna	subsp. *perviridis* Bailey	Leaves/inflorescences
E. Asia	Pak choi	subsp. *chinensis* (L.) Hanelt	Leaves
E. Asia	Napa cabbage	subsp. *pekinensis* (Lour.) Hanelt	Leaves
E. Asia	Choy sum/Caixin	var. *parachinensis* (L.H. Bailey) Hanelt	Leaves/inflorescences
E. Asia	Mizuna	subsp. *nipposinica* (L.H. Bailey) Hanelt	Leaves
E. Asia	Tatsoi/Wutacai	subsp. *narinosa* (L.H. Bailey)	Leaves
E. Asia	Taicai	subsp. *chinensis* Makino var. *tai-tsai* Hort	Leaves
E. Asia	Zicaitai	var. *purpuraria* (L.H. Bailey) Kitam	Leaves/inflorescences
Europe	Rapini/Broccoletto	subsp. *sylvestris* L. Janch. var. *esculenta* Hort	Leaves/inflorescences
Eurasia	Turnip rape	subsp. *oleifera* (DC.) Metzg	Seeds
Eurasia	Turnip	subsp. *rapa*	Root-hypocotyl, leaves
Eurasia	Wild field mustard	subsp. *sylvestris* (L.) Janch.	Leaves/inflorescences

Despite the global economic importance of *B. rapa* as a crop species, many aspects of its domestication are contested, including the number of domestication events, first crop type(s) domesticated, location(s) and timing of domestication, and pattern of subsequent selection for morphologically diverse crops. Past genetic studies of *B. rapa* have recovered conflicting patterns of morphological and genetic similarity across Eurasia. While some studies show that morphologically similar crops (e.g., oilseeds) are closely related to each other despite being geographically distant (Zhao et al., 2010; del Carpio et al. 2011; Tanhuanpää et al., 2015), others find that geographically proximal crops are closely related despite strong morphological differences (Song et al. 1988, 1990; Zhao et al. 2005; Takuno et al. 2007; Annisa et al. 2013; Guo et al. 2014; Del Carpio et al. 2011). The geographically disparate but morphologically similar *B. rapa* crops in Europe and Asia have led some researchers to propose multiple domestication events (e.g., Song et al., 1988; Zhao et al., 2005; Sinskaya 1928), but others support a single domestication (Burkill 1930; Song et al., 1990; Ignatov et al., 2008; Qi et al., 2017).

It is unclear whether the first domesticate resembled turnips, leafy forms, or oilseed forms, as archaeological and literary evidence attests to the antiquity of all three (Table 2). Proposed locations of domestication areas include Europe (Song et al., 1988, 1990; Zhao et al., 2005), Central Asia (Ignatov et al., 2008; Qi et al., 2017), and East Asia (Song et al., 1988; Zhao et al., 2005). Timing of domestication has been difficult to assess due in part to the relative difficulty of finding and identifying *Brassica* seeds at archaeological sites (but see Allchin, 1969; Hyams, 1971), but literary, linguistic, and genetic evidence have provided some insight (Table 2). The history of selection for different crops following domestication is also debated. For example, some have suggested that napa cabbage was bred from pak choi (Song et al. 1990; Zhao et al. 2005; Takuno et al. 2007), while others have suggested an origin in East Asian turnips (McGrath and Quiros, 1990), and crosses between pak choi and East Asian turnips (Li 1981; Ren et al. 1995; Song et al., 1980; Qi et al., 2016). Several *B. rapa* flower and leaf crops exist in northwestern Spain and Portugal (Francisco et al., 2009; Obregón, 2016), but their origins have not been investigated.

Table 2. Archaeological, linguistic, literary, and genetic evidence for the antiquity of *B. rapa* crop types. Sources: 1) Ignatov and Artemyeva, 2008 2) Prakash and Hinata, 1980 3) Prakash et al., 2001 4) Li, 1981 5) Ye, 1989 6) Luo, 1992 7) Leach, 1982 8) Körber-Grohne, 1987 9)Qi et al., 2017.

Approximate Date	Location	Crop type	Type of evidence	Source
Neolithic	Switzerland, India, China	Turnip	Archaeology	1, 2
7000-6000 BCE	Western Eurasia	Turnip	Linguistic	1
~3000 BCE	China	General	Literary	3
2600 BCE	China	Turnip	Literary	4, 5, 6
1500 BCE	India	Oilseed	Literary	2, 3
800 BCE	Assyria	Turnip	Literary	7
700 BCE	Babylonia	Turnip	Literary	8
659 CE, 1061 CE	China	Napa cabbage	Literary	9

Insights into the domestication of *B. rapa* have been limited due to a lack of knowledge about wild forms (McAlvay, Chapter 1). Wild crop relatives can help clarify the location and timing of domestication events (Vavilov 1926, 1951; Harlan 1971; Mykal et al., 2011; Meyer et al., 2012) Although field mustard (*B. rapa* ssp. *sylvestris*) occurs spontaneously on roadsides, waste areas, farmlands, and riversides in many temperate areas worldwide (Wilkinson et al. 2003; Hall et al., 2005; Andersen et al., 2009), it is unclear whether these populations are feral crop escapes or truly wild forms (Crouch et al., 1995; Andersen, 2009; McAlvay, Chapter 1). Our inability to differentiate wild and feral forms of *B. rapa* also threatens the persistence of wild populations which could be reduced by increased agricultural weed control in its native range (Hall et al., 2005; McAlvay, Chapter 1). Identifying wild crop relatives also contributes to resources for breeding and food security (Maxted et al., 2008; Jansky et al., 2013; Brozynska et al., 2016). Wild relatives of crops have proven useful in plant breeding for resistance to biotic and abiotic stresses (Flis et al., 2005; Hajjar and Hodgkin, 2007; Honnay et al., 2012; Dempewolf et al., 2014) partly because breeding can cause diversity bottlenecks in domesticated organisms (Tanksley and McCouch, 1997; Feuillet et al., 2008; Olsen and Gross 2008).

To clarify the domestication history and wild or feral status of *B. rapa,* we performed genotyping-by-sequencing (GBS) (Elshire et al., 2011) on a panel of *B. rapa* crops and spontaneously growing samples to assess demography, genetic structure and diversity. We addressed the following questions: 1) Are spontaneously occurring *B. rapa* populations wild or feral? 2) when, where, and how many times was *B. rapa* domesticated? 3) what was the first crop type domesticated? and 4) what are the origins of the Mediterranean leafy/inflorescence crops grelos and rapini?

We also modeled the distribution of spontaneously occurring *B. rapa* in Eurasia and North Africa during the mid-Holocene to address the following question: what areas would have been suitable for the climatic niche of wild *B. rapa* at the putative time of domestication?

Methods

Genetic analyses

Sampling—We obtained 289 *B. rapa* and outgroup samples through seed banks (USDA, IPK-Gatersleben), fieldwork in Mexico, and directly from researchers (Supp. material 1). GBS data from these samples were combined with a previously generated GBS diversity dataset (Bird et al., 2017), providing a total of 653 samples before sample filtering. This diversity panel incorporates samples from six continents and 12 crop subspecies. We did not include three East Asian vegetable crops (caixin, zicaitai, taicai), which whole-genome-resequencing data suggests were selected from pak choi (Cheng et al. 2016). Our panel augments Bird et al.'s (2017) sampling of East Asian leafy crops, South and Central Asian oilseeds (S/C Asian oilseeds), and European turnips by adding turnips from West and Central Asia (C/W Asia; defined as Asia between Pakistan and Turkey), and Europe, Mediterranean leafy crops (Spanish grelos and Italian rapini), and spontaneously occurring samples from Europe, the Caucasus, the Americas, and New Zealand. Seeds and/or young leaf material collected from Mexico were collected on the permit of Dr. Robert Bye for the CONABIO based project "*Conservación de la agrobiodiversidad de la Milpa Tarahumara, Chihuahua.*" If seeds were the only materials collected at a site, they were grown at the University of Wisconsin-Madison Walnut Street greenhouse facility in 6" square pots, and Promix HP medium (Premier Tech, Rivière-du-Loup, Québec) and DNA was extracted from young leaf material. Herbarium specimens were deposited in the WIS herbarium, with duplicates in the MEXU herbarium in the case of Mexican specimens.

Table 3. Crop types, locations, and numbers of samples included in final dataset.

Category	**Crop/location**	**Sample #**
Turnips	N. African	3
	Spanish	5
	Central/Western (C/W) Asian	14
	Turkish	10
	European	25
	East Asian	10
Leafy crops	Choy sum	14
	Pak choi	46
	Mizuna, Tatsoi, Komatsuna	5
	Napa cabbage	154
	Rapini (Italy)	12
	Grelos (Spain)	11
Oilseeds	Southern/Central (S/C) Asian	74
	European	2
	East Asian	1
Spontaneously occurring	Europe	22
	Caucasus	6
	Latin American	161
Outgroup	Outgroup (B. oleracea)	1

DNA extraction and sequencing—The University of Wisconsin-Madison Biotechnology Center (UWBC) extracted DNA from leaf material using the CTAB method (Doyle and Doyle 1987) and generated GBS data. The restriction enzyme ApeKI was used to construct GBS libraries. Samples were 96-plexed in each of three lanes of Illumina HiSeq 2000 (Illumina Inc. San Diego, CA, United States), and one well in each plate was left blank as a negative control. Raw sequence data were combined with sequences from Bird et al. (2017) and processed using the GBS 2 pipeline in Tassel 5 (Glaubitz et al., 2014). Parameters used for the pipeline can be found in supplementary materials 2. Reads were aligned to the publically available *B. rapa* ssp. *pekinensis* v1.5 reference genome (Wang et al., 2011) using Burrows-Wheeler Alignment (Li and Durbin, 2009). Raw reads will be publically available on the National Center for Biotechnology Information Sequence Read Archive (NCBI SRA).

SNP and sample filtering—The SNPs resulting from the Tassel 5 pipeline were filtered using VCFtools (Danecek et al., 2011) based on read depth (minimum mean depth = 3), number of alleles (only biallelic loci used), minimum number of genotypes scored per site (100% for PCA, 90% for all other analyses) and for all analyses except for demographic modeling, set the minimum minor allele frequency to 5%. We used Tassel 5 to filter SNP sites for a maximum heterozygosity of 50% and remove taxa that had <50% of the loci scored or were negative control blanks. Samples identified by Bird et al. (2017) to be *B. napus* or otherwise problematic were removed. To validate subspecies labeling we followed the protocol of Guo et al. (2014) and grew each of the 289 original accessions in the University of Wisconsin-Madison Walnut Street Greenhouses.

Diversity—To determine patterns of diversity within subgroups of *B. rapa*, we evaluated nucleotide diversity (Nei and Li, 1979) in Tassel 5 (Glaubitz et al., 2014) and variance within and across groups using the Analysis of Molecular Variance (AMOVA) (Excoffier et al., 1992) in Arlequin 3.5 (Excoffier et al., 2005).

Genetic structure—To determine the genetic structure of *B. rapa*, we used fastSTRUCTURE 1.0, a Bayesian approach able to rapidly analyze large numbers of samples with genome-wide data (Raj et al. 2014). The *Brassica oleracea* outgroup sample was omitted for this analysis. We ran fastSTRUCTURE at group (K) values between 1 and 20 and used the ChooseK.py script included in the fastSTRUCTURE package to assess the K value that maximized marginal likelihood. FastSTRUCTURE plots were generated using the online utility STRUCTURE PLOT 2.0 (Ramasamy et al., 2014). To further investigate the genetic structure of the samples, we used principal component analysis (PCA) in Plink 1.07 (Purcell et al., 2007) and visualized the resulting ordination using Genesis PCA and Admixture plot viewer (Buchmann and Hazelhurst, 2014). To evaluate genetic differentiation among groups, we calculated F_{ST} (Weir and Cockerham, 1984) between each pair of groups defined by subspecies and geography using Arlequin 3.5 (Excoffier et al., 2005).

***Tree-based analyses*—**In order to visualize the hierarchical structure of the species, we generated a Neighbor-Joining tree (Saitou and Nei, 1987) using Nei's genetic distance and 100 bootstrap replicates in Paup 4.0 (Swofford, 2003). We also used coalescent-based SVDquartets (Chifman and Kubatko, 2014) implemented in PAUP 4.0 (Swofford, 2003) to generate a species tree estimate. SVDquartets evaluates quartets of taxa and combines them to infer the most likely tree. We evaluated all possible quartets and produced 100 bootstrap replicates. Clades were defined based on subspecies classification and geography.

***Demographic analysis*—**In order to investigate population branching structure, population size shifts, and migration between populations in spontaneously occurring Caucasian samples, Central/Western Asian turnips, and East Asian turnips we created and tested demographic models using *moments* (Jouganous et al. 2017, Gutenkunst et al. 2009). For this analysis, we did not filter for minimum minor allele frequency as it can skew the site-frequency-spectrum (Linck and Battey 2017). We constructed the joint allele frequency spectrum for the three populations. Because numerous SNPs might not be called in every individual in each population, we projected sample sizes down to include more SNPs in each analysis (Marth et al. 2004). To reduce the risk of model over-parameterization, we assumed a single population size change for each population and no more than two migration rates. We used the built-in likelihood-based optimization functions in *moments* to fit demographic model parameters to the data. Confidence intervals were computed using the Godambe information matrix, which attempts to correct test statistics to account for any effects of linkage between SNPs (Coffman et al. 2016). To estimate the timing of splitting events, we used an effective population size of 30000 and one generation per year.

Species Distribution modeling

Species distribution modeling uses species occurrence data and geoclimatic information to predict the potential distribution of a species in an area (Kozak et al., 2008, Nakazato et al., 2010). We used georeferenced *B. rapa* occurrence data from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org) and 19 bioclimatic variables (Supp. materials, 3) with 2.5-minute spatial resolution from WorldClim Version 1.4 (Hijmans et al., 2005, http://www.worldclim.org). We modeled the niche of spontaneously occurring *B. rapa* and predicted compatible habitat given the CCSM4 mid-Holocene climate model in MaxEnt (Phillips et al., 2006). Model performance was evaluated with the adjusted area under receiver operating characteristic (ROC) curve (DeLong et al., 1988). To ensure that the occurrence data included only non-crop *B. rapa*, we removed occurrences without location data and included only samples with location data suggesting weedy or wild habitat. Occurrences were included that were on roadsides, in ditches, waste areas, abandoned fields, railroad tracks, parklands, mentioned weediness, or were classified as subspecies *campestris* or *sylvestris*. Our search on GBIF for *Brassica rapa* returned 34,361 occurrences. After removing occurrences with no geographical data, 21,425 remained. Removing occurrences with crop subspecies resulted in retention of 21,089 occurrences. Samples with no information detailing the environment of the sample were removed resulting in 10,130 occurrences. Filtering for occurrences with environmental information suggesting a weedy or wild habit thinned our occurrences to 2263. To reduce bias in sampling that may arise from collecting in accessible areas close to population centers, we removed samples occurring within 100km of each other using the spThin R package (Aiello-Lammens et al., 2015). Spatial thinning resulted in a final dataset of 638 occurrences. Omission rate on training samples was close to predicted omission and the receiver operating characteristic curve (DeLong et al., 1988) showed an area under curve of 0.960, suggesting that the model fit the data reasonably well.

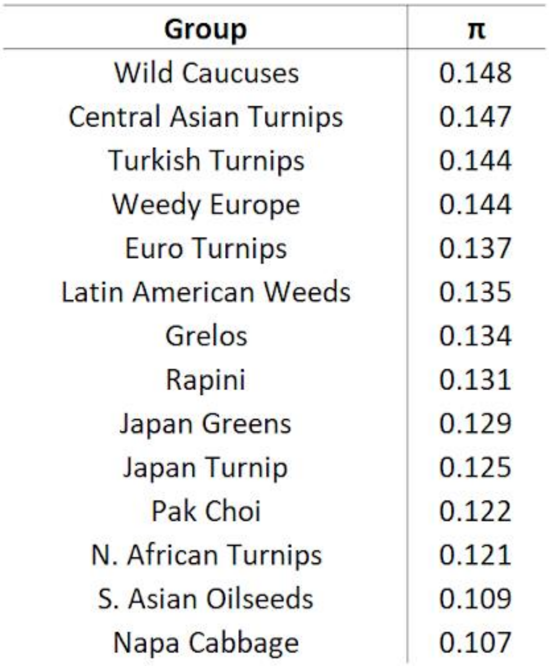
Results

Genotyping-by-sequencing

***SNP calling, SNP filtering, and sample filtering*—**Sequencing produced 656,335,837 raw reads (average 218,778,612 per lane) were combined with the 823,954,356 from Bird et al. (2017). A total of 372,182 SNPs were called using the Tassel pipeline. After downstream SNP and sample filtering, 49,460 SNPs and 573 taxa (Table 3) remained.

***Diversity*—**Nucleotide diversity (Table 3) within subgroups of *B. rapa* indicates higher diversity in samples from Central and Western Asia, intermediate levels of diversity in European crops and weeds, and lowest diversity in East Asian crops and South Asian oilseeds.

Table 4. Nucleotide diversity of *Brassica rapa* accessions by crop type and geographical region.



Group	π
Wild Caucuses	0.148
Central Asian Turnips	0.147
Turkish Turnips	0.144
Weedy Europe	0.144
Euro Turnips	0.137
Latin American Weeds	0.135
Grelos	0.134
Rapini	0.131
Japan Greens	0.129
Japan Turnip	0.125
Pak Choi	0.122
N. African Turnips	0.121
S. Asian Oilseeds	0.109
Napa Cabbage	0.107

***Genetic structure*—**The ChooseK function in fastSTRUCTURE suggested a K value of 6 maximized marginal likelihood. At K = 6, pak choi, napa cabbage, European crops and weeds, Latin American weeds, and South Asian oilseeds showed distinct grouping. Canadian weedy samples emerged in the same group as European crops and weeds, while Latin American weeds formed a distinct group with some contributions from the European crops and weeds group. Spontaneously occurring *B. rapa* from the Caucasus were associated with European crops and weeds, but also showed contributions from Asian turnips and oilseeds. Central/West Asian turnips were associated with European crops and weeds but also with East Asian turnips and South/Central Asian oilseeds. Some of the South/Central oilseeds formed a discrete group, while others clustered with Asian turnips.

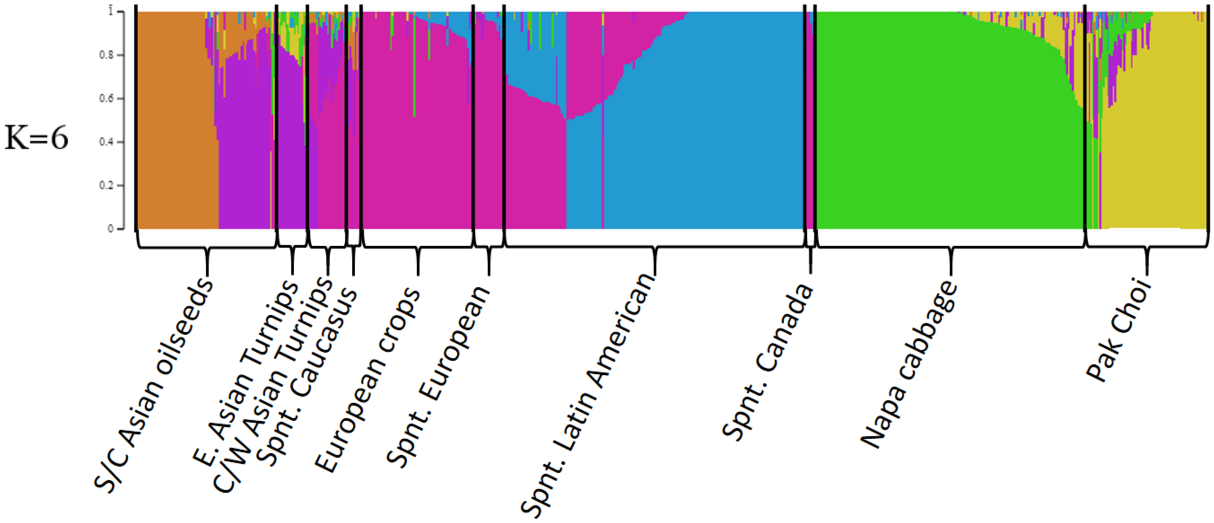


Figure 1. fastSTRUCTURE plot indicating population structure of *Brassica rapa* crops and weeds at K=6. Each color represents a population/group. Each column represents a single individual and its proportion of ancestry from a given population.

The PCA analysis generally separated samples based on geography and crop type. PC1 separated European, Asian, and Latin American samples geographically. PC2 separated South Asian oilseeds from East Asian leafy types. Spontaneously occurring forms from the Caucasus mountains clustered around the *B. oleracea* sample, while spontaneous forms from the rest of Europe and the Americas were closely affiliated with European turnips and Mediterranean leafy types. Among East Asian crops, turnips emerged as most closely associated with the *B. oleracea* sample. Among Central/West Asian crops, turnips were also most closely associated with the outgroup. Mediterranean leafy crops emerged in a cluster with European turnips and weeds.

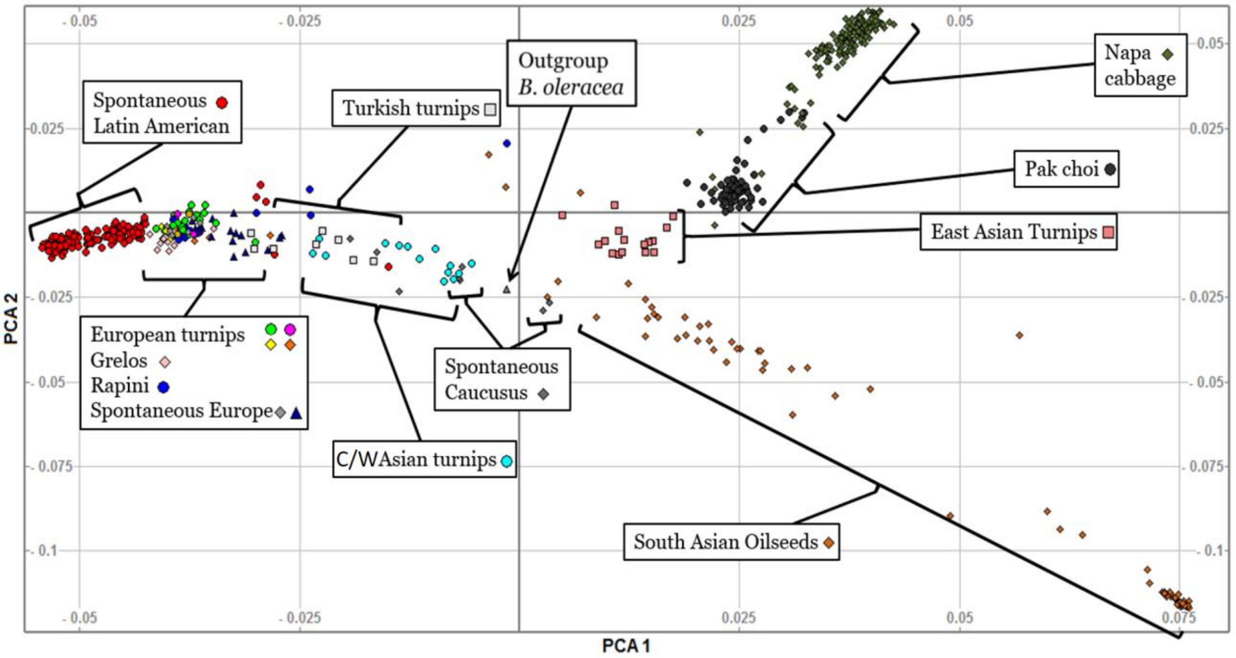
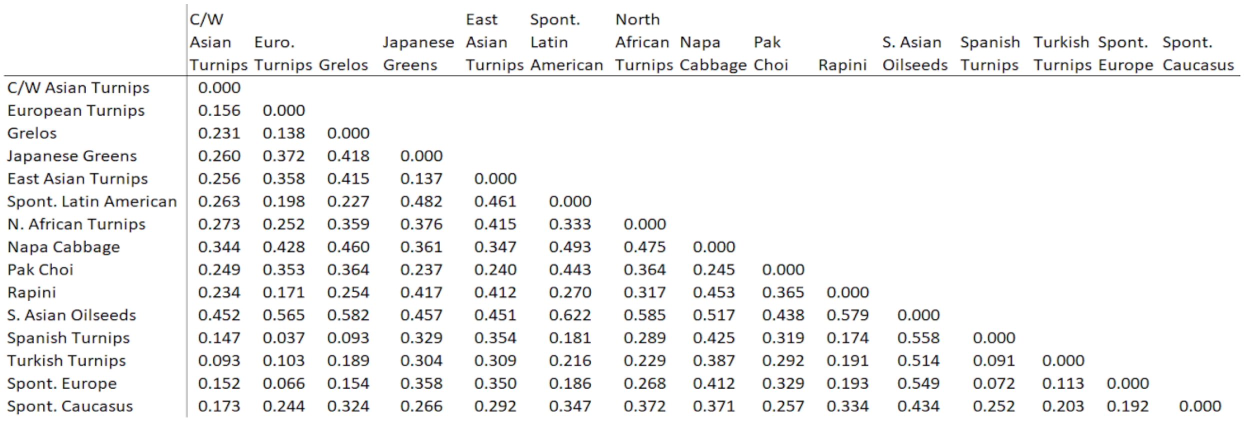


Figure 2. PCA of *Brassica rapa* samples. Each icon represents a geographic/subspecific category. PC1 explains 45.07% of the variance and PC2 explains 22.92% of the variance.

F_{ST} values among populations ranged from .622 between South Asian Oilseeds and Latin American weeds to .037 between Spanish turnips and other European turnips (Table 3). Grelos were least differentiated from Spanish turnips and Rapini were least differentiated from other European turnips. South Asian oilseeds were relatively highly differentiated from all other groups (all values >0.4). Latin American weeds showed lowest differentiation from Spanish Turnips (0.181) and European weeds (0.186). Spontaneously occurring populations in the Caucasus were least differentiated from Central/West Asian turnips.



	C/W Asian Turnips	Euro. Turnips	Grelos	Japanese Greens	East Asian Turnips	Spont. Latin American	North African Turnips	Napa Cabbage	Pak Choi	Rapini	S. Asian Oilseeds	Spanish Turnips	Turkish Turnips	Spont. Europe	Spont. Caucasus
C/W Asian Turnips	0.000														
European Turnips	0.156	0.000													
Grelos	0.231	0.138	0.000												
Japanese Greens	0.260	0.372	0.418	0.000											
East Asian Turnips	0.256	0.358	0.415	0.137	0.000										
Spont. Latin American	0.263	0.198	0.227	0.482	0.461	0.000									
N. African Turnips	0.273	0.252	0.359	0.376	0.415	0.333	0.000								
Napa Cabbage	0.344	0.428	0.460	0.361	0.347	0.493	0.475	0.000							
Pak Choi	0.249	0.353	0.364	0.237	0.240	0.443	0.364	0.245	0.000						
Rapini	0.234	0.171	0.254	0.417	0.412	0.270	0.317	0.453	0.365	0.000					
S. Asian Oilseeds	0.452	0.565	0.582	0.457	0.451	0.622	0.585	0.517	0.438	0.579	0.000				
Spanish Turnips	0.147	0.037	0.093	0.329	0.354	0.181	0.289	0.425	0.319	0.174	0.558	0.000			
Turkish Turnips	0.093	0.103	0.189	0.304	0.309	0.216	0.229	0.387	0.292	0.191	0.514	0.091	0.000		
Spont. Europe	0.152	0.066	0.154	0.358	0.350	0.186	0.268	0.412	0.329	0.193	0.549	0.072	0.113	0.000	
Spont. Caucasus	0.173	0.244	0.324	0.266	0.292	0.347	0.372	0.371	0.257	0.334	0.434	0.252	0.203	0.192	0.000

Table 4. F_{ST} values across geographic/subspecific categories of *Brassica rapa*. Spont. indicates spontaneously occurring populations.

The neighbor-joining tree showed spontaneously occurring *B. rapa* from the Caucasus mountains were positions closest to the outgroup. Central/Western Asian turnips were sister to a cluster that included European turnips, European and Latin American spontaneously occurring samples, European oilseeds, and Mediterranean leafy crops. A single turnip sample from the Republic of Georgia in the Caucasus emerged as sister to this cluster. Within the cluster of Central/Western Asian turnips, turnips from the Hindu Kush in Afghanistan, Pakistan, and Tajikistan were sister to the other samples. Spanish turnips formed a grade leading up to the Spanish leafy grelos samples. North African turnips formed a cluster sister to Italian leafy rapini accessions. Overall, both spontaneously occurring *B. rapa* and oilseed types each emerged in three distinct parts of the tree. European oilseeds were sister to a large cluster of European turnips, and our single East Asian oilseed sample was sister to all East Asian leafy vegetables. The South and Central Asian oilseeds (sarsons and toria) emerged in a grade leading up to a cluster of sarsons with short branches. A single turnip accession from Pakistan was sister to all East Asian crops and a cluster of East Asian turnips was sister to East Asian oilseeds and leafy crops.

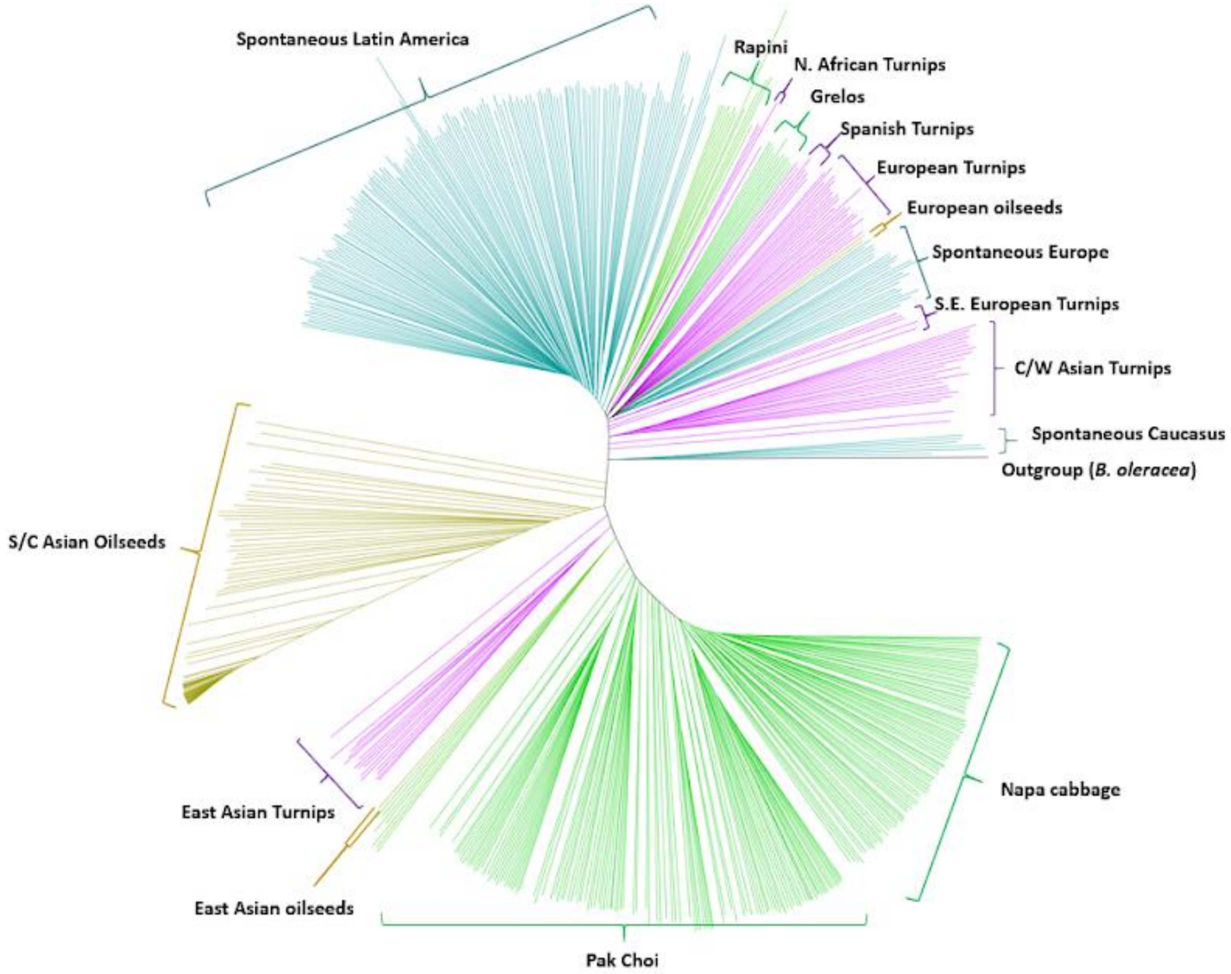


Figure 4. Neighbor-joining tree of relationships between *B. rapa* crops and spontaneously occurring accessions. Colors of branches on the tree represent crop types and crop/spontaneously occurring status. Green branches indicate leafy crop types, purple indicates turnip crop types, gold indicates oilseed crop types, and turquoise indicates spontaneously occurring samples.

The SVDquartets coalescent tree topology was largely congruent with the neighbor-joining tree, with some exceptions: rapini and North African turnips did not form a clade, and spontaneously occurring Latin American *B. rapa* samples were sister to a clade of grelos and Spanish turnips. Low bootstrap support was found at nodes toward the base of the tree, as well as the node separating European turnips from Spanish crops and Latin American weeds.

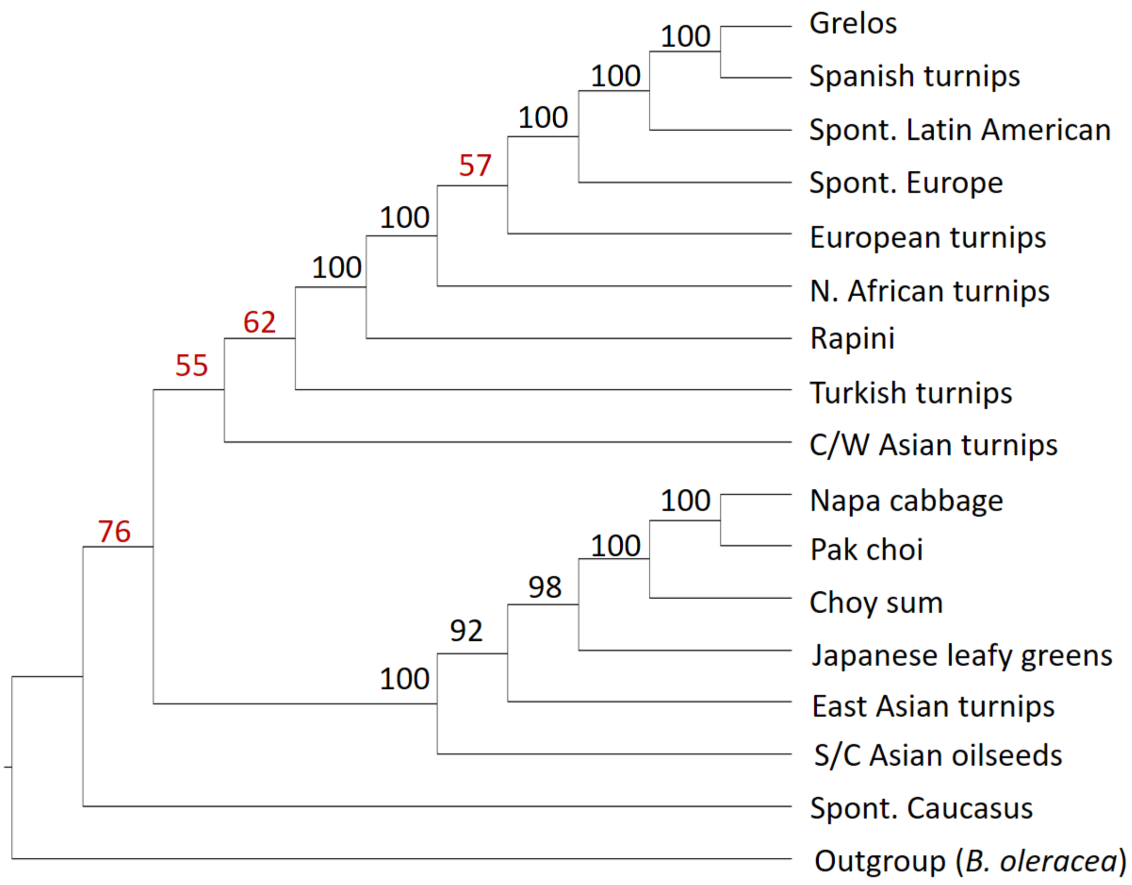


Figure 5. SVDquartets coalescent tree of *Brassica rapa* based on crop types and geography. Branch lengths are not meaningful in this analysis. Bootstrap values below 90 are highlighted in red.

***Demographic modeling*—**The model that had the highest likelihood for fitting the data (Figure 6.) was a scenario in which spontaneously occurring *B. rapa* from the Caucasus split off from the Central/Western Asian and East Asian turnips around 5,712 YBP and Central/Western and East Asian turnips split from each other around 1,982 YBP. Most of the migration in the model was from the Caucasus population to the turnips, though there was some migration the the Caucasus populations between the turnip types. According to the model, the effective population size of the spontaneously occurring Caucasian population experienced a dramatic reduction in size around 1,982 YBP. East Asian turnips also experienced a reduction in N_e at the same time. Exact model parameters and residuals of fits can be found in supplementary material 9.

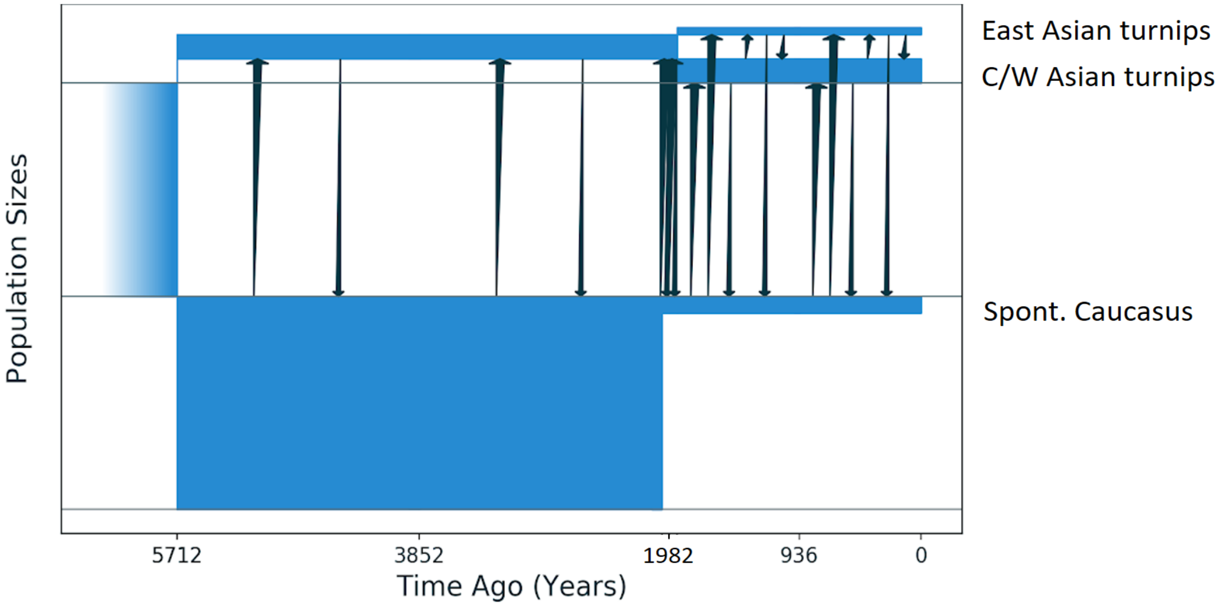


Figure 6. Demographic model of population splits, migration events, and effective population sizes through time for East Asian turnips, Central/Western Asian turnips, and spontaneously occurring *B. rapa* from the Caucasus. Black arrows indicate direction and timing of migration. Relative width of arrows indicates amount of migration. The height of the blue bars indicates relative effective population sizes.

Species Distribution Modeling

Our niche model for *B. rapa* found the following bioclimatic variables to be most important for describing its distribution: precipitation seasonality (coefficient of variation) (43.3%), isothermality (mean diurnal temperature range/temperature annual range) (13.7%), precipitation of driest month (9.6%), and mean temperature of warmest quarter (8.7%). The model predicting

B. rapa distribution under a mid-Holocene climate scenario (Fig. 7) indicated suitable habitat in a nearly contiguous band from Iberia, North Africa, and the British Isles to coastal China. This strip of area mainly followed highland formations, except in Europe, where coastal areas were also of high suitability. A potential gap in suitable habitat was present in the present-day borderlands of Afghanistan and Iran.

Figure 7. Mid-Holocene niche model for *Brassica rapa* in Eurasia and northern Africa. Darker areas indicated better niche fit for spontaneously occurring *B. rapa.*

Discussion

***Wild B. rapa in the Caucasus*—**The positions of the crop and spontaneous populations of *B. rapa* in our fastSTRUCTURE analysis, PCA, and coalescent tree, and demographic model suggests that our sampling of spontaneously occurring *B. rapa* in Turkey, Russia, and Georgia represents truly wild material. This is consistent with Sinskaya's (1969) suggestion that wild forms exist in the Caucasus mountains. The Caucasus region is a putative center of domestication for parsnips (Rubatzky et al. 1999) and an important reservoir of wild relatives of crops such as parsnips and spinach. Our niche models indicated that habitat for *B. rapa* around the Caucasus would be suitable under a mid-Holocene climate model (Fig. 7). We also found highest diversity in the wild Caucasian samples and Southwest Asian turnips. The identification of the Caucasus as a region where wild *B. rapa* grows further highlights the need for conservation measures and collecting trips in this area. Conserving these pools of diversity will be important in the future to cope with changing environmental conditions (Guarino and Lobell 2011). Identifying wild *B. rapa* material provides a valuable source of alleles of agronomic interest for *B. rapa* crops and other *Brassica* species. This includes the allotetraploids *B. napus* (rutabagas, leafy greens, and rapeseed) and *B. juncea* (leaf mustard and oilseeds) for which *B. rapa* is a genome donor (Qian et al., 2006; Mei et al., 2011). Diversity bottlenecks from polyploidization and domestication in these crops have resulted in limited diversity for agronomic improvement (Cowling 2007). Identifying wild forms of *B. rapa* also allow future studies to investigate the genetic basis of changes under domestication in this species. The characteristics of the wild ancestor of *B. rapa* crops were previously unclear. For example, it was unclear whether it was annual or biennial, formed swollen root hypocotyls or not, and was self-incompatible or self-compatible. Our phenotyping for subspecies identification indicated that wild samples from the Caucasus were annual and did not form swollen root-hypocotyls.

***Feral B. rapa in Europe and the Americas*—**While the genetic structure, diversity, and tree-based analyses suggest that spontaneously occurring forms from the Caucasus are wild, these analyses supported a feral origin for spontaneous *B. rapa* in the Americas and Europe. European weedy samples emerged in association with European crops in PCA, fastSTRUCTURE, and the NJ and coalescent trees, and had relatively low differentiation from European crops in the F_{ST} analysis. FastSTRUCTURE analysis in McAlvay (Chapter 3) suggests that admixture between wild *B. rapa* and European crops may have led to the feral weedy forms. Despite lower levels of diversity among the feral samples, their local adaptation to biotic and abiotic stresses could make them a valuable source of breeding material as in feral rice (Li et al., 2017).

***Initial crop type and location(s) of domestication in __B.__ __rapa__*—**In our genetic structure analyses, turnips from Central/Western Asia appear to be most closely associated with wild forms and had the highest levels of nucleotide diversity of any crop group. This is consistent with the suggestions of McGrath and Quiros (1990) and Siemonsma and Piluek (1993) that turnips were the first domesticated *B. rapa* crop. In the neighbor-joining tree, a single turnip sample from the Republic of Georgia was sister to all Central/Western Asian turnips and European *B. rapa*, either indicating admixture between Caucasian turnips and wild populations or suggesting that this area could have been important for the domestication of turnips. Except for this potentially anomolous or admixed sample, the samples from the Hindu Kush in Afghanistan, Pakistan, and Tajikistan came out sister to the rest of the *B. rapa* samples from West Asia and Europe.

As can be seen in the PCA, fastSTRUCTURE, and F_{ST} analyses, East Asian turnips are associated with the wild samples and Central/Western Asian turnips. East Asian turnips also emerge as sister to other East Asian crops in our tree-based analyses consistent with the phylogeny created by Bird et al. (2017). In our neighbor-joining tree, a single turnip accession from Pakistan was sister to all East Asian crops, though admixture between subspecies could explain its position. This suggests the possibility of a common origin of all turnip crops around the Hindu Kush, but further sampling of crop and wild *B. rapa* would be necessary to support this conclusion. Our demographic model suggested a relatively recent (~2000 YBP) split between East Asian and Central/Western Asian turnips. This late split, however, contradicts literary evidence indicating the presence of turnips in China as far back as 4600 YBP (see Table 2). Our mid-Holocene distribution model is consistent with domestication occurring in highland Asia but does not refute previous hypotheses of a European origin. A lack of spontaneous *B. rapa* present in East Asia (De Candolle 1886; McGrath and Quiros, 1992) suggests that domestication may not have occured in in this area, though the original range of *B. rapa* may have extended into East Asia in the past (Whyte, 1983).

Oilseed crops appear to have at least three independent origins. While our NJ tree and SVDquartets analyses show South/Central Asian oilseeds from the Hindu Kush in Afghanistan, Pakistan, and India as more closely associated with East Asian crops, they are associated with Central, West, and East Asian turnips in fastSTRUCTURE. The South/Central Asian oilseeds that clustered most closely with wild forms in PCA were *B. rapa* ssp. *dichotoma* from Pakistan and Afghanistan, while *B. rapa* ssp. *trilocularis* were mainly from India and formed a closely related discrete group further away from wild forms in both analyses. These findings are consistent with an origin in or around the Hindu Kush, as was predicted for Central Asian, West Asian, and European crops and weeds above. Low levels of diversity recovered in the South/Central Asian oilseeds may be due to their self-compatibility as is the case in other self-compatible organisms (Charlesworth and Wright, 2001; López-Villalobos & Eckert, 2018). Our findings are consistent with South/Central Asian oilseeds arising from an independent domestication event (Zhao et al., 2005; Warwick et al., 2008) or from early selection on turnips. This contradicts the conclusions of Song et al. (1988), who concluded that South/Central Asian oilseeds were derived from European oilseeds. One scenario that is consistent with our results would be an initial cultivation of *B. rapa* in the Hindu Kush, with subsequent local differentiation of self-compatible oilseed forms and biennial turnip crops. Our limited sampling of oilseeds from East Asia (1 sample) and Europe (2 samples) limit our inferences. We, like Reiner et al. (1995), found European oilseeds closely associated with European turnips.

Parallel selection for leafy crops out of turnip crops—Our findings are also consistent with three parallel selection events for leafy forms out of turnip forms in Europe and East Asia. Turnip types in both Europe and East Asia consistently emerged as sister to clades containing leafy crops in those areas in tree-based analyses. The enlarged root-hypocotyl of turnips is controlled by relatively few genes and may have therefore been lost multiple times through human selection and/or ferality (McGrath and Quiros 1991). The position of the Mediterranean leafy crops, Spanish grelos and Italian rapini, in our tree-based analyses suggests two independent origins from turnips. While rapini is sometimes classified as *B. rapa* ssp. *sylvestris,* implying an affinity with wild forms, we found that rapini samples were more closely related to turnip crops, in agreement with the results that Qi et al. (2017) found using RNA-sequencing data. Our analyses showed an association between North African turnips and rapini suggesting a possible Trans-Mediterranean introduction of turnips or leafy types into Italy. In our SVDquartets analyses, Spanish grelos are closely affiliated with Spanish turnips, and in our neighbor joining tree, Spanish turnips form a grade leading to a clade of grelos, providing evidence that grelos were independently selected from local turnip crops. The position of East Asian turnips in the neighbor-joining and coalescent trees suggests that this pattern of selecting leafy crops out of turnip crops may also have taken place in East Asia.

Timing of domestication event(s)—Our demographic analysis indicated a split between wild *B. rapa* and turnip crops roughly 5700 YBP. While this prediction is sensitive to our estimates of initial effective population size and generation time, this finding is consistent with archaeological and linguistic evidence (Table 2). The word for turnip reconstructs in Proto-Indo-European (PIE) as *reps (Pokorny, 1959; but see Iversen and Kroonen, 2017) and Proto-Indo-European is estimated to have been spoken as early as 4348 YBP (Holman et al., 2011), suggesting that this crop may have been domesticated before that time. Several hypotheses on the location of Proto-Indo-European-speakers exist, but many scholars support their placement in Anatolia (Bouckaert et al., 2012) or the Pontic-Caspian steppe north of the Caucasus (Gamkrelidze and Ivanov 1995; Renfrew, 1987). Linguistic evidence for oilseeds in India dates to around 3500 YBP, supporting an early domestication or selection for South/Central Asian oilseed crops.

Diffusion of B. rapa crops throughout Eurasia and N. Africa—Our fastSTRUCTURE analysis, PCA, and tree-based analyses are consistent with a spread of *B. rapa* crops throughout Eurasia from a Central or Western Asian origin. Our fastSTRUCTURE diagram at K=6 is consistent with serial subsampling of crop groups starting with wild *B. rapa* in Central or Western Asia being selected for turnip crops and oilseed crops, each with substantial contributions from a common ancestral population (shown in purple in Fig. 1). The fastSTRUCTURE analysis is also consistent with an origin of pak choi and/or napa cabbage from the East Asian turnip forms and spread of Central or Western Asian turnips to Europe. Subsampling leading to European leafy crops and weeds can more clearly be seen in McAlvay (Chapter 3, Fig. 2). PCA supports this sequence of events, showing a trifurcating pattern centering around *B. oleracea* and wild Caucasian samples. The three arms are as follows: 1) Central/West Asian turnips closest to center followed by Turkish turnips, European crops and weeds, and Latin American weeds, 2) East Asian turnips closest to center, followed by pak choi and napa cabbage, and 3) Pakistani and Afghani *B. rapa* ssp. *dichotoma* oilseeds closest to center followed by Indian *B. rapa* ssp. *trilocularis*. Our NJ tree supports a similar route of spread, with Central/West Asian turnips (including Turkish turnips) close to wild forms, followed by southeastern European turnips, and the remaining European and Latin American crops and weeds. The spread of turnips from Anatolia to southeastern Europe is consistent with archaeological records showing the diffusion of technology and agriculture through the same route (Özdoğan (2011).

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Chapter 3
Reconstructing the dedomestication and invasion history of field mustard (*Brassica rapa*)

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Abstract

Biological invasions can drive ecological change and impact agricultural production. Reconstructing the invasion history of weedy plant populations contributes to the understanding of dispersal and range expansion as well as biological control. Field mustard, a weedy form of the crop species *Brassica rapa* has colonized croplands, waste areas, and roadsides in temperate regions worldwide. Its status as an economically important crop plant has led to considerable genomic tools, making it a potential model to study invasion genetics. The origins, route(s) of invasion, diversity, and genetic structure of weedy forms are poorly understood. Here, we used a combination of genotyping-by-sequencing data and niche modeling to reconstruct the dedomestication and invasion history of *B. rapa* in the Americas, Europe, and New Zealand and model the potential distribution of *B. rapa* worldwide. Levels of diversity in the invaded and native range were comparable, with relatively high diversity in the invasive Argentine, Colombian, and Canadian weeds. Tree-based and genetic structure analyses indicated an affiliation between European/Canadian feral forms and European turnips, with evidence for introgression from wild forms. Latin American and New Zealand weeds were closely associated with each other and with European turnips and weeds, but also with European leafy crops.

Keywords: Invasion, invasive species, feral, crop wild relative

Introduction

We define an invasive species as one that expands beyond its native range and affects local biodiversity and resources (Kolar and Lodge 2001). Invasive species threaten local ecosystems, biodiversity, and agricultural production (Richardson and Pyšek, 2006; Prentis et al., 2007, Pyšek et al. 2012; Pyšek and Richardson 2011; Vilà et al. 2011) and cause approximately $100,000,000,000 in damage to crops and ecosystem functions (Pimental et al., 2005). Reconstructing the histories of biological invasions provides important information for the control of invasive species (Estoup and Guillemaud, 2010; Roderick and Navajas, 2003; Garcia-Rossi et al., 2003; Müller-Schärer et al., 2004; Goolsby et al., 2006; Zalucki et al., 2007; Stewart et al., 2009), general insights into how species colonize new areas, and the foundation for studying local adaptation in invasive species (Hierro et al., 2005; Sax et al. 2007; Prentis et al., 2008; Dlugosch and Parker, 2008).

In some cases, invasive species are wild or feral forms of crop plants (Hegde et al., 2006; Gressel, 2005). Examples of crops with weedy forms include grapes (DeAndreas et al. 2012), parsnips (Tania et al., 2015), rice (Li et al., 2017), radishes (Ridley et al. 2008), carrots (Magnussen and Hauser, 2007) and millet (Darmency, 2005). Dedomestication, the process of crops becoming feral, can occur by different routes. Feral plants may be derived from domesticated material (endoferal) or originate from domesticated material that has introgression from wild or feral relatives (exoferal) (Gressel, 2005). While wild crop relatives in their native range have been utilized extensively for breeding material (Hajjar and Hodgkin 2007), invasive crop relatives have been neglected as a source of germplasm for breeding material, (Li et al., 2017) despite potential rapid adaptation of invasive species to new environments (Prentis et al., 2008; Dlugosch and Parker, 2008). While often lacking desirable agronomic traits such as yield and indehiscence, these weedy populations are often tolerant of stresses that hamper growth of crops (Li et al., 2017). Disentangling the origins and spread of invasive crop relatives is the first step to understanding their local adaptation and potential utility in building resilient germplasm.

Field mustard (*Brassica rapa* L. Brassicaceae: $2n = 20$) includes both cultivated and weedy forms, but the precise origins of the latter are unclear. In Eurasia, *B. rapa* was domesticated and selected for morphologically diverse crop forms (e.g., turnips, bok choi, napa cabbage, and oilseeds), making it a model of phenotypic diversification under artificial selection (Gómez-Campo and Prakash, 1999; Zhao et al., 2005; Guo et al., 2014; Bird et al., 2017; Qi et al., 2017; McAlvay, Chapter 2). Field mustard, the spontaneously occurring form of this species (*B. rapa* ssp. *sylvestris*) has become an agricultural weed in temperate regions worldwide (Chèvre 2004; Gressel 2005; Hall 2005). Genetic evidence suggests that field mustard consists of a combination of feral and truly wild populations, but details surrounding their origin and spread remain unclear (Andersen et al., 2009; McAlvay, Chapter 2). For example, field mustard in much of Europe, the Americas, and New Zealand appears to have a feral origin (McAlvay, Chapter 2), but it is unclear whether it is endoferal or exoferal. While field mustard is often outcompeted by other plants in low-disturbance ecosystems (Plant Biotechnology Office, 1999), it can be problematic in high-disturbance areas such as croplands and is considered a noxious weed in 11 U.S. states (AKEPIC, 2012). It frequently competes with crop plants and forms large seed banks in the ground with discontinuous germination (Basu et al., 2004), requiring multiple years of removal to control populations (DiTomaso and Healy, 2007). Experimental evidence also supports mild allelopathic effects in weedy populations (Bye, 1979).

The origins and route(s) of invasion of exotic populations of *B. rapa* are unclear. In the Americas weedy *B. rapa* can be found from from Canada to Argentina, especially in highlands and coastal areas with a Mediterranean climate. Historical records suggest an early colonial introduction of *B. rapa* to Latin America (Gade, 1972; Bye, 1979). Weedy forms are often associated with grain fields (Pickering, 1879; Ridley, 1930; Barreau, 2016; McAlvay, Chapter 4) and may have been introduced as a contaminant in grain barrels imported to the Americas and distributed by missionaries (Gade, 1972; Bye, 1979). This route of introduction would likely have resulted in large propagule numbers and multiple influxes of native material over time, which could have increased invasion success and/or reduced the founder effect on genetic diversity (Lockwood et al., 2005; Ross et al. 2008). Alternatively, turnip rape brought as an oil source (Bye, 1979) or turnips brought as fodder (Pers. Comm, Paul Williams) by the Spanish may have escaped from cultivation. Finally, like distillation technology (Valanzuela-Zapata et al., 2014), Asian *B. rapa* crops or weeds may have arrived through the Manila galleon trade that connected the Philippines and Mexico between the 16th and 19th centuries.

Following its introduction to the Americas, weedy forms of *B. rapa* have been adopted as food, medicine, and fodder by cultures ranging from northwestern Mexico to Patagonia (Gade, 1972; Berlin et al., 1974; Bye, 1979; Ladio, 2001; Vieyra-Odilon and Vibrans, 2001; McAlvay, Chapter 4). These cultures engage in a variety of plant management practices including intentional sparing of plants from weeding and sowing seeds in fertilized plots (Bye, 1979; Gade, 1972; Vieyra-Odilon and Vibrans, 2001).

While paleontological evidence (MacDonald, 1993), and biological collections (e.g., Chauvel et al., 2006; Pyšek and Prach, 1995; Crawford and Hoagland, 2009), provide useful information about invasion histories (Estoup and Guillemaud, 2010), population genetics has recently become an important tool (Sakai et al., 2001; Stewart et al., 2009; Estoup and Guillemaud, 2010; Lombaert et al. 2011; Cristescu, 2015). Population genetics not only contributes to reconstructing routes of invasion, but also helps clarify the genetic diversity, admixture, and source population(s) of the invader (reviewed in Estoup and Guillmaud 2010). Due to the availability of extensive genomic infrastructure, weedy field mustard presents a powerful study system for understanding weed genomics (Basu et al., 2004).

There are substantial genetic tools available for study of *B. rapa* due to its status as an economically important crop plant, including at least two reference genomes (Wang et al., 2011; Amasino and Woody unpublished), and there are additional benefits due to its close relationship to *Arabidopsis thaliana*, a model species for plant genetics (Paterson et al., 2001, Yang et al., 2005). As a result, weedy field mustard has been used frequently as in studies of transgene flow from crops to wild relatives, specifically from *B. napus* crops to weedy *B. rapa* (e.g., Chèvre 2004; Warwick et al., 2003; Warwick et al., 2008). Despite its importance as an agricultural weed, little is known about the diversity, origins, and population structure of field mustard (Andersen et al., 2009). Also, while the presence of spontaneously occurring *B. rapa* globally is attested by occurrence data (GBIF.org [Accessed February 8, 2018]), its climatic niche and distribution have not been explicitly modeled, limiting the ability to identify areas of potential invasion by weedy forms and areas where crop wild relatives may occur McAlvay (Chapter 1).

To investigate the origins, distribution, diversity, and genetic structure of weedy *B. rapa* worldwide, we combined niche modeling and genotyping-by-sequencing (GBS) (Elshier et al., 2011) data to investigate the niche, genetic structure, and diversity of spontaneously occurring *B. rapa*. We addressed the following questions: (1) what is the origin of weedy forms of *B. rapa*? (2) what is the source and route of introduction of weedy *Brassica rapa* in the Americas and New Zealand? (3) was there a reduction in diversity upon introduction of *B. rapa* into the Americas, and (4) what is the climatic niche and distribution of weedy *B. rapa* worldwide (5) do the predicted niches of *B. rapa* based on Eurasian occurrences differ from predictions based only on Latin American occurrences?

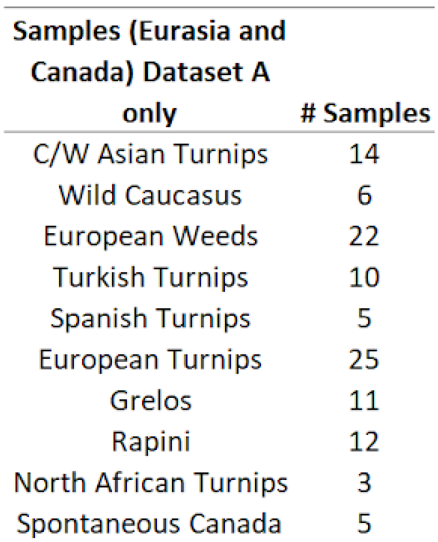
Materials and Methods

Genetic analyses

Sampling—In our genotyping-by-sequencing analysis, we included samples from the Americas, New Zealand, Europe, North Africa, and Southwest Asia (Table 1, Supplementary material 4) as previous analyses strongly suggest an origin for invasive *B. rapa* in European, North African, or Central/West Asian crops or weeds (Bird et al., 2017; Qi et al., 2017; McAlvay, Chapter 2), we omitted East and South Asian crops from our analyses. We obtained *Brassica rapa* and outgroup samples through seed banks (USDA, IPK-Gatersleben), fieldwork in Latin America, and directly from researchers (Supp. material 4). These data were combined with a previously generated GBS diversity set (Bird et al., 2017). Samples were divided into two groups for the purpose of analyses. We used dataset **A** (270 samples) to investigate the origins of *B. rapa* weeds worldwide. This group includes includes western Eurasian crops and weeds as well as invasive *B. rapa* from the Americas and New Zealand. We used dataset **B** (161 samples) to trace the spread of field mustard throughout Latin America, California (U.S.A.) and New Zealand. Dataset B includes samples from Latin America and California (U.S.A.), as well as a single sample from New Zealand. Latin American and Californian sampling can be seen in Fig. 1). Historical evidence supports an early colonial introduction of *B. rapa* (Gade, 1972; Bye, 1979) at a time when California would have been under Spanish or Mexican control, so we include California in Latin America for the purposes of this paper. The New Zealand sample was included in dataset B due to a close association with Latin American populations recovered in genotyping-by-sequencing analyses in McAlvay (Chapter 2). One sample of *Brassica oleracea* was included as an outgroup in tree-based analyses. All samples used represent a subset of the those included in McAlvay (Chapter 2).

Table 1. Number of *B. rapa* samples from regions and crop types by dataset. C/W Asian turnips indicates Central/Western Asian turnips.

Samples (Spont. Latin America and N.Z.) Dataset A/B	**# Samples**
Argentina	3
Chile	1
Bolivia	3
Ecuador	2
Peru	2
Colombia	2
Guatemala	2
Panama	3
Honduras	1
Eastern Mexico	9
Central Mexico	11
N.W. Mexico	12
Southern Mexico	8
California	3
New Zealand	1



Samples (Eurasia and Canada) Dataset A only	**# Samples**
C/W Asian Turnips	14
Wild Caucasus	6
European Weeds	22
Turkish Turnips	10
Spanish Turnips	5
European Turnips	25
Grelos	11
Rapini	12
North African Turnips	3
Spontaneous Canada	5

Figure 1. Map of *B. rapa* individuals sampled in Latin America**.** The Chilean sample and Californian samples were in coastal regions, while all other samples were in highland regions above 2000 meters. We considered samples from Ecuador, Peru, Bolivia, and Chile as a group called “Andes”. Map data: 2018 Google, INEGI

DNA extraction and sequencing—Genotyping-by-sequencing and SNP calling was conducted as in McAlvay (Chapter 2). Briefly, DNA was extracted using CTAB (Doyle and Doyle 1987) and sequenced using an Illumina HiSeq 2000 (Illumina Inc. San Diego, CA, United States). Library construction used the restriction enzyme ApeKI. We used the GBS 2 pipeline in Tassel 5 (Glaubitz et al., 2014) to process reads and call single nucleotide polymorphisms (SNPs) and Burrows-Wheeler Alignment (Li and Durbin, 2009) to align reads to a reference genome (Wang et al., 2011).

SNP and sample filtering—To develop a high-quality SNP panel, we separately filtered SNPs called via the Tassel 5.0 GBS 2 pipeline for dataset A and dataset B with the following

VCFtools (Danecek et al., 2011) parameters: minimum mean depth = 3, only biallelic loci, minimum of 90% of genotypes scored per site (100% for principal component analysis), and minimum minor allele frequency of 5%. To remove poorly sequenced individuals, samples were removed that had <50% of the loci scored.

***Genetic diversity*—**We evaluated nucleotide diversity (Nei and Li, 1979) in Tassel 5 (Glaubitz et al., 2014) and variance within and across groups in dataset A using the Analysis of Molecular Variance (AMOVA) (Excoffier et al., 1992) in Arlequin 3.5 (Excoffier et al., 2005). Statistical significance of variance components from AMOVA were evaluated using Arlequin 3.5 with 1000 permutations. Groups for AMOVA were defined as South America, Central America, and Mexico.

***Genetic structure*—**We assessed the population structure in datasets A and B using fastSTRUCTURE 1.0 (Raj et al. 2014). To evaluate the number of groups (K) that optimized marginal likelihood, we tested fastSTRUCTURE runs between 1 and 20 with the python ChooseK.py script included in the fastSTRUCTURE. Plots of fastSTR5UCTURE results at K values surrounding the optimal K were produced with STRUCTURE PLOT 2.0 (Ramasamy et al., 2014). On each dataset, we conducted principal component analysis (PCA) in Plink 1.07 (Purcell et al., 2007) and produced plots using Genesis PCA and Admixture plot viewer (Buchmann and Hazelhurst, 2014). We calculated genetic differentiation among groups using fixation indices (F_{ST}; Weir and Cockerham, 1984) between each pair of geographical groups in Arlequin 3.5 (Excoffier et al., 2005). The *Brassica oleracea* outgroup sample was omitted for the above analyses.

***Neighbor-joining, coalescent, and TreeMix trees*—**We used two tree-based analyses to investigate the relationships between samples and groups of samples for dataset A. We generated a Neighbor-Joining tree (Saitou and Nei, 1987) using Nei's genetic distance and 100 bootstrap replicates in Paup 4.0 (Swofford, 2003). We used SVDquartets (Chifman and Kubatko, 2014) implemented in Paup (Swofford, 2003) to produce a coalescent tree based on evaluation of all possible quartets of relationships with 100 bootstrap replicates. Clades for SVDquartets were predetermined based on geographic regions. Neighbor-joining and coalescent analyses were rooted using the *B. oleracea* sample. We used TreeMix (Pickrell and Pritchard, 2012) to identify patterns of gene flow between subspecies and geographical areas. TreeMix uses a maximum likelihood method to construct trees and a Gaussian model of genetic drift (Pickrell and Pritchard, 2012). Clades were defined as in the SVDquartets analysis. TreeMix outputs are sensitive to the number of migration events designated (Malinksy et al., 2017) so we ran TreeMix with the number of migration events designated between zero and five. For our TreeMix analysis we divided European and Canadian weeds into three different clades recovered in the neighbor-joining tree.

Niche modeling

To investigate niches of *B. rapa* in the native and invaded range, we generated the following three models: A) a global projection using spontaneously occurring samples from Eurasia to train the model, B) a global projection using Latin American samples to train the model, and C) a global projection using samples from across the global range of *B. rapa* to train the model. We carried out species distribution modeling using contemporary climate models in MaxEnt (Phillips et al., 2006) with georeferenced *B. rapa* occurrence data from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org) and 19 bioclimatic variables (Supp. material 3) with 2.5-minute resolution from WorldClim Version 1.4 (Hijmans et al., 2005, http://www.worldclim.org). We filtered and thinned our occurrence data as in McAlvay (Chapter 2) and partitioned our data into Eurasian and Latin American occurrences. Occurrence filtering resulted in 134 western Eurasian occurrences for training model A, 198 Latin American occurrences for training model B, and 449 worldwide occurrences for training model C. Model performance was evaluated with the adjusted area under receiver operating characteristic curve (DeLong et al., 1988).

Results

Genetic analyses

***GBS sequencing and filtering*—**Details of read number and read mapping can be found in McAlvay (chapter 2, this dissertation). After filtering dataset **A** contained 35,348 SNPs and dataset **B** contained 33,084 SNPs

***Genetic Diversity*—**Nucleotide diversity (Table 1) appears to be highest in non-Andean South America, Canada, and Central America. Intermediate levels are found in the Andes, Central Mexico, and California. Lowest levels of nucleotide diversity are seen Northwestern, Eastern, and Southern Mexico. As a whole, western Eurasian samples had higher nucleotide diversity than weedy populations in the Americas, although the most diverse groups in the Americas (Argentina, Colombia, Canada, and Central America) were more diverse than European crop types.

Table 1. Nucleotide diversity of weedy field mustard in the Americas and of western Eurasian crops, feral populations, and wild samples.

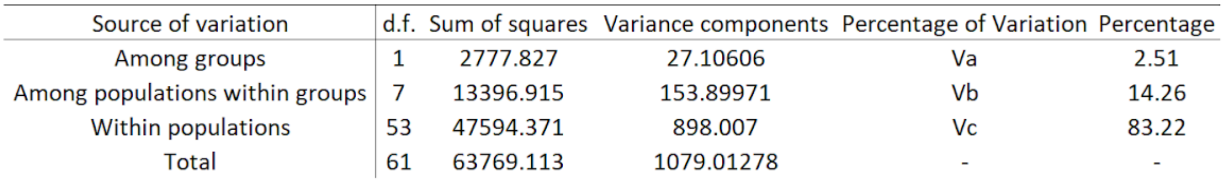
Samples (Weedy Americas)	π
Argentina	0.234
Colombia	0.232
Canadian weeds	0.232
Central America	0.231
Andes	0.222
Central Mexico	0.221
California	0.220
Northwestern Mexico	0.213
Eastern Mexico	0.209
Southern Mexico	0.207
All Americas	0.222

Samples (Western Eurasian)	π
C/W Asian Turnips	0.239
Wild Caucasus	0.238
European Weeds	0.236
Turkish Turnips	0.235
Spanish Turnips	0.229
European Turnips	0.224
Grelos	0.219
Rapini	0.214
North African Turnips	0.196
All Western Eurasian	0.243

The AMOVA analysis of dataset B (Table 2) investigated hierarchical partitioning of diversity across populations and the following three regions: Mexico, Central America, and South

America and indicated 83.22% of variance was within populations, 14.26% among populations in groups, and 2.51% among groups.

Table 2. Results of AMOVA analysis of Dataset B comparing *Brassica rapa* populations in Mexico, Central America, and South America.



Source of variation	d.f.	Sum of squares	Variance components	Percentage of Variation	Percentage
Among groups	1	2777.827	27.10606	Va	2.51
Among populations within groups	7	13396.915	153.89971	Vb	14.26
Within populations	53	47594.371	898.007	Vc	83.22
Total	61	63769.113	1079.01278	-	-

For dataset A, fastSTRUCTURE's ChooseK function identified K=4 as the optimal number of clusters to maximize marginal likelihood and K=9 to explain the structure in the data. The analysis (Fig. 2) showed that at K=4, rapini, Latin American weeds, European turnips/grelos, and Southwest Asian/wild Caucasian samples formed discrete groups. At K=5, grelos separated from the European turnip group and rapini merged with the European turnip group, while wild Caucasian samples formed their own group. European weeds showed some admixture with the wild Caucasus group. At K=6, Grelos, Rapini, and Caucasian wild samples formed relatively discrete groups. At all levels between K=4 and K=6, European and Canadian weeds were in the same cluster as European turnips, whereas North African turnips appeared to be heavily admixed, typically appearing as a composite of SW Asian turnips, Rapini, and Latin American weeds.

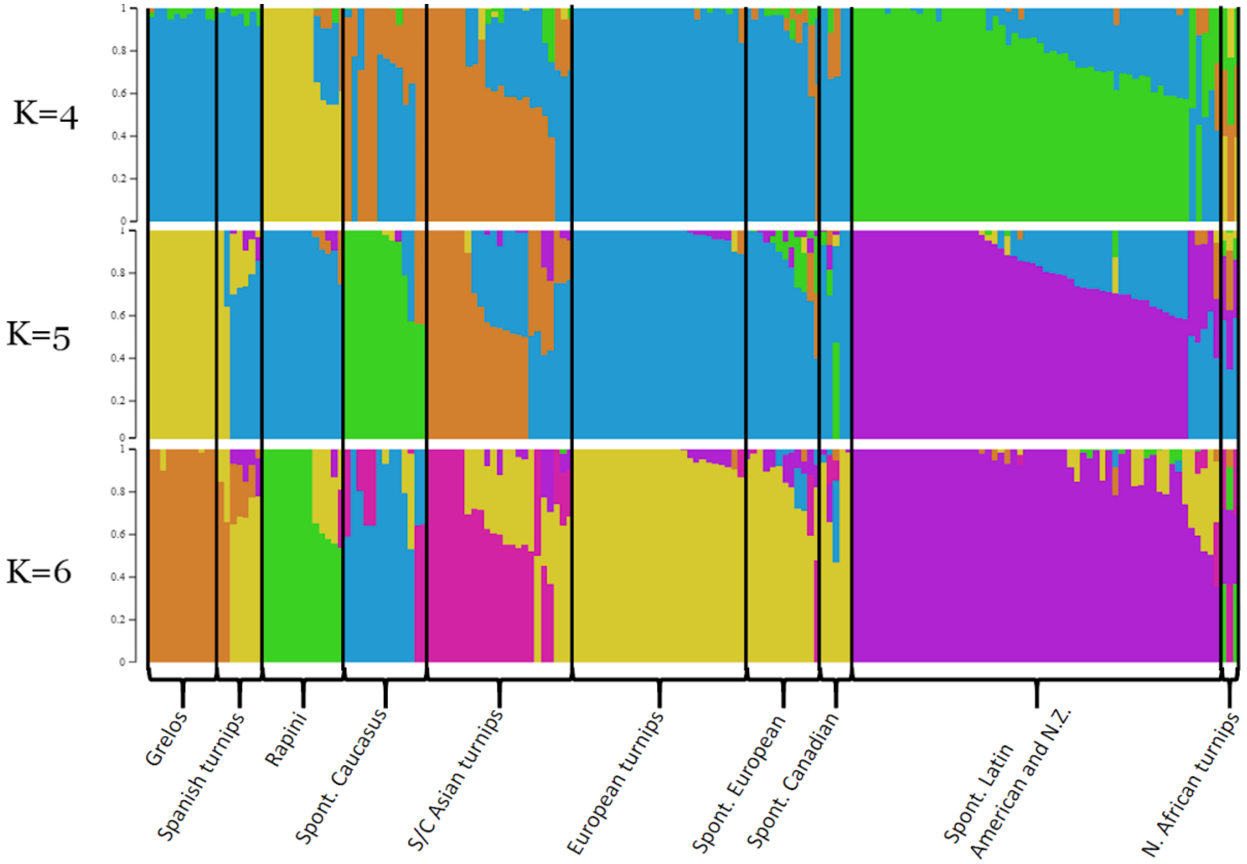


Figure 2. fastSTRUCTURE plot of dataset A indicating population structure of *Brassica rapa* crops and weeds at three different values of K. Each color represents a population/group. Each column represents a single individual and its proportion of ancestry from a given population. “Spont.” refers to spontaneously occurring samples.

For dataset B, fastSTRUCTURE’s ChooseK.py script identified K=1 as the optimal number of clusters to maximize marginal likelihood and K=3 to explain the structure in the data. The analysis (Fig. 3) showed that at K=2, samples from Mexico formed a group, though Central and Eastern Mexico had substantial contributions from the other group consisting of all other populations. At K=3, Southern Mexican samples formed a discrete group with no admixture, at K=4, Eastern Mexican samples formed a group, at K=5, Central Mexican samples formed a group, and at K=6 Andean and Californian samples formed a cluster.

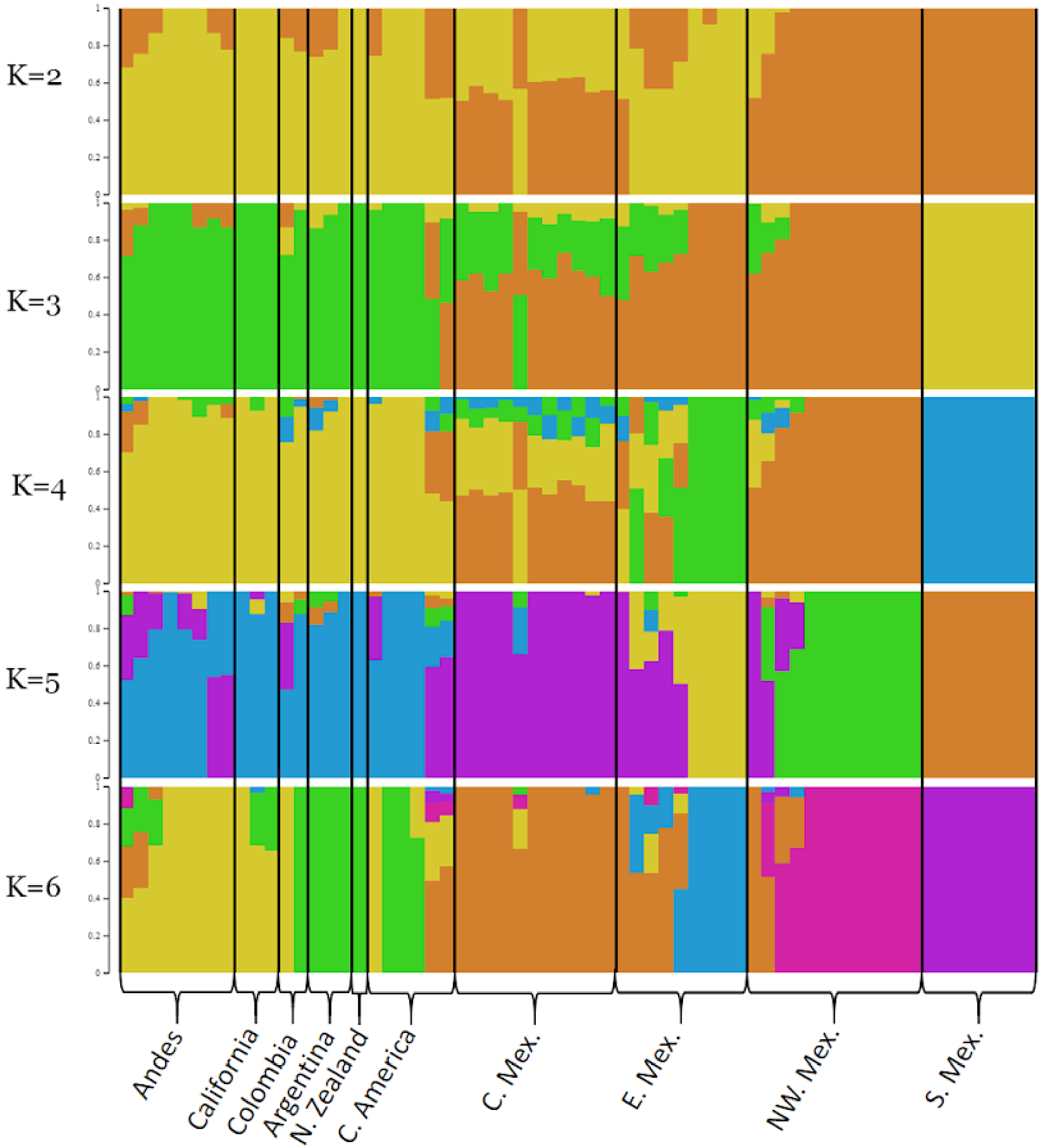


Figure 3. fastSTRUCTURE plot of dataset B indicating population structure of *Brassica rapa* weeds at three different values of K. Each color represents a population/group. Each column represents a single individual and its proportion of ancestry from a given population.

Our PCA for dataset A (Fig 4) showed three clusters: 1) Canadian weeds, European turnips, Mediterranean leafy vegetables, and European weeds, 2) Latin American weeds, 3) Wild Caucasian samples and Central/Western Asian turnips. Some European weeds were intermediate between cluster 1 and cluster 3. The New Zealand sample was intermediate between groups 1 and 2. North African samples emerged in their own small group intermediate between the other three. Among Latin American samples, individuals from Argentina and Panama were most closely associated with the other groups, while those of eastern Mexico were the most distant from groups 1 and 3. PC1 separated groups geographically, while PC2 separated North African turnips and European turnips from the cluster of European crops and weeds.

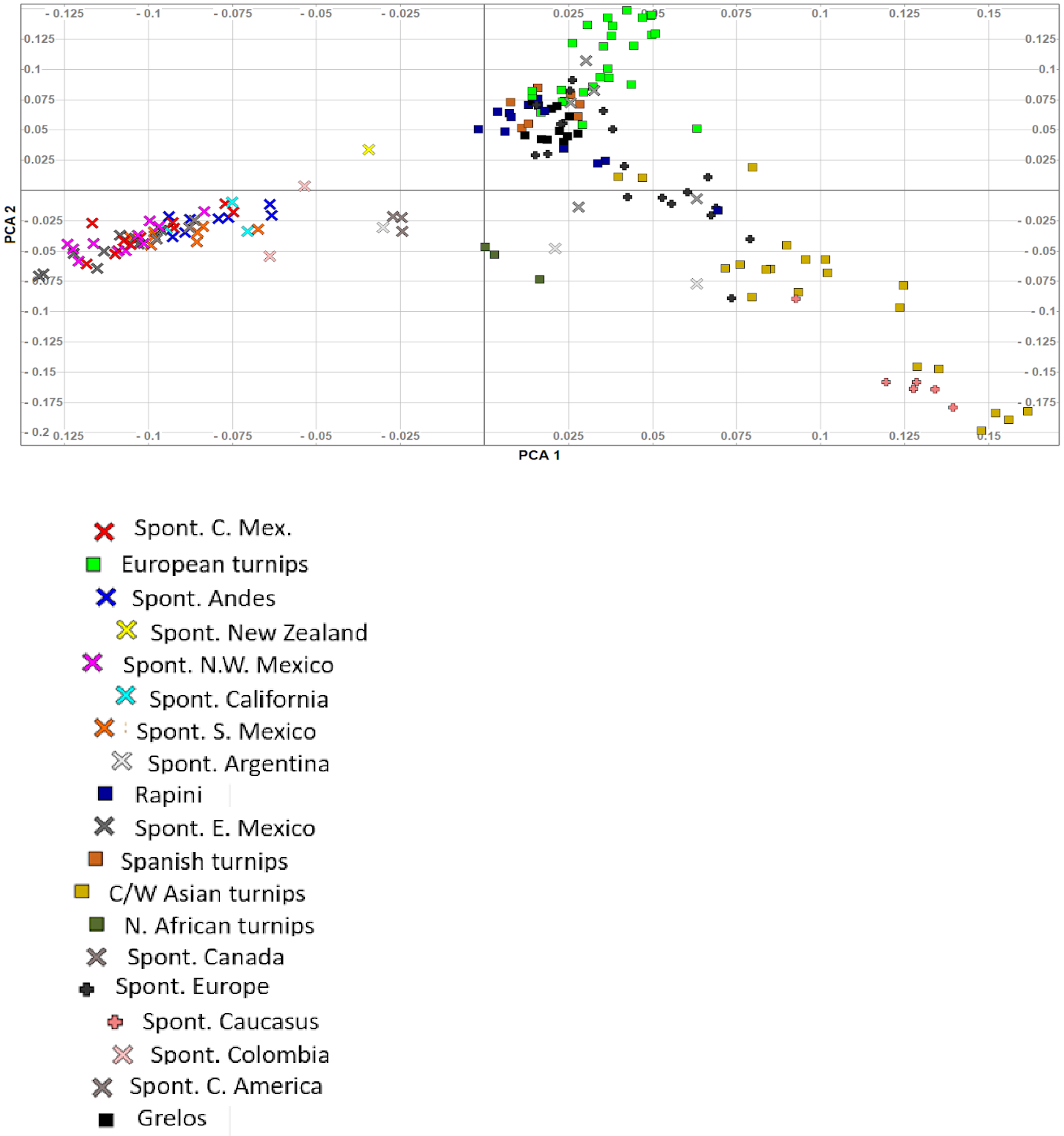


Figure 4. PCA of *Brassica rapa* in dataset A. Each icon represents a geographic/crop category. “X” symbols indicate spontaneously occurring *B. rapa* outside of Eurasia, “+” symbols indicate spontaneously occurring *B. rapa* within Eurasia, and squares indicate domesticated *B. rapa*. PC1 explains 25.58% of the variance and PC2 explains 11.21% of the variance.

The PCA for dataset B (Fig. 5) showed separation of Central Mexican, NW Mexican, and Eastern Mexican groups from South American, New Zealand, and Californian samples across PC1. PC2 separated Eastern and N.W. Mexican samples from each other and separated southern Mexican samples from South and Central American samples.

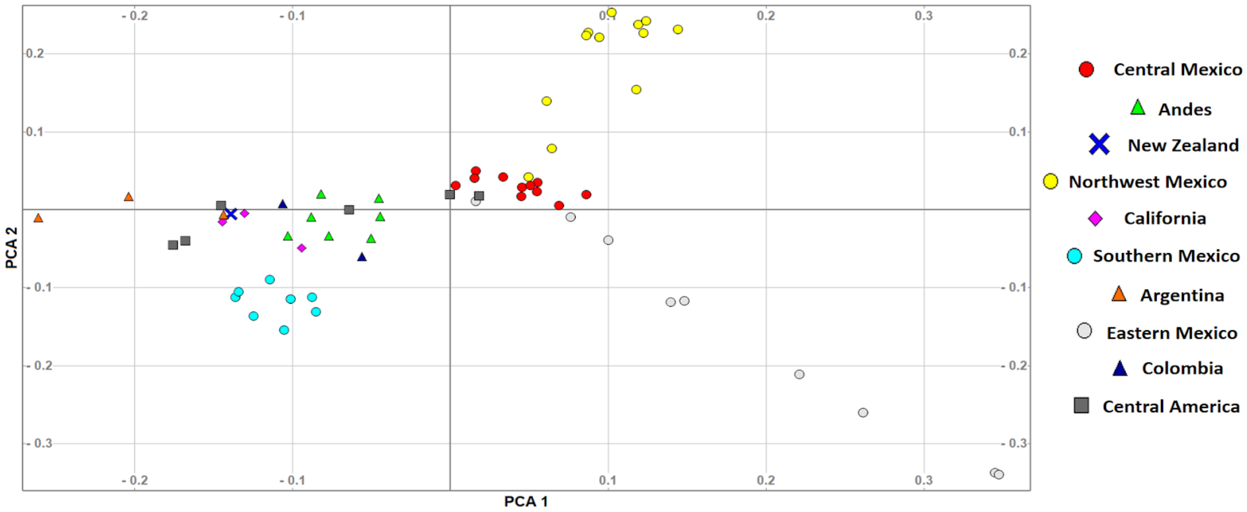


Figure 5. PCA of *Brassica rapa* in dataset A. Each icon represents a geographic/crop category. Circle symbols indicate Mexican samples, square symbols indicate Central American samples, triangle symbols indicate South American samples, diamond symbols indicate samples from the United States, and “x” symbols indicate samples from New Zealand. PC1 explains 65.61% of the variance and PC2 explains 11.53% of the variance.

F_{ST} calculated for all pairs of populations in dataset A (Supp. materials 5) ranged from -0.020 (effectively 0) between Southwest Asian turnips and Argentinian feral populations to 0.346 between Northwest Mexican feral populations and New Zealand feral populations. Canadian weeds were least differentiation from European weeds (0.004), samples from California were least differentiated from Andean weeds,

Neighbor joining and coalescent trees—The neighbor-joining tree of dataset A recovered clusters similar to the PCA. Spontaneous European samples were separated by Southern European turnips but were in the cluster of European crops and weeds. Spontaneously occurring *B. rapa* in from Argentina and Colombia was sister to the rest of the clade that included Latin American and New Zealand weeds. Of the Latin American weeds, only Californian samples formed a discrete cluster.

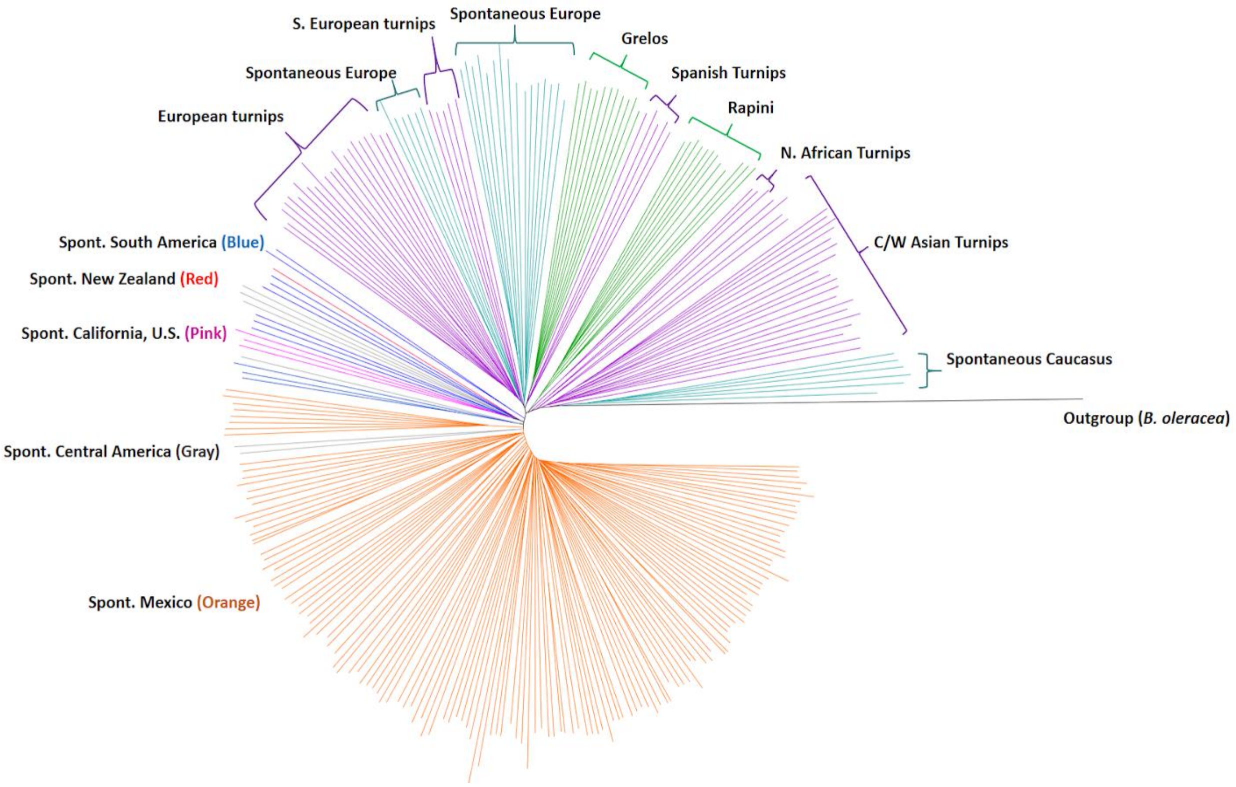


Figure 6. Neighbor-joining tree demonstrating relationships between *B. rapa* crops and spontaneously occurring accessions. Green indicates leafy crop types, purple indicates turnip crop types, turquoise indicates spontaneously occurring samples from Eurasia, blue indicates spontaneous samples from South America, red indicates spontaneous samples from New

Zealand, pink indicates spontaneous samples from California, gray indicates spontaneous samples from Central America, and orange indicates spontaneous samples from mexico.

The species tree topology produced from SVDquartets differed from the neighbor-joining tree and results found in McAlvay (Chapter 2). The coalescent tree showed European and Canadian weeds as sister to all crops and invasive samples. This analysis also clustered Argentinian feral populations with North African turnips. New Zealand weeds emerged in a clade with Californian populations.

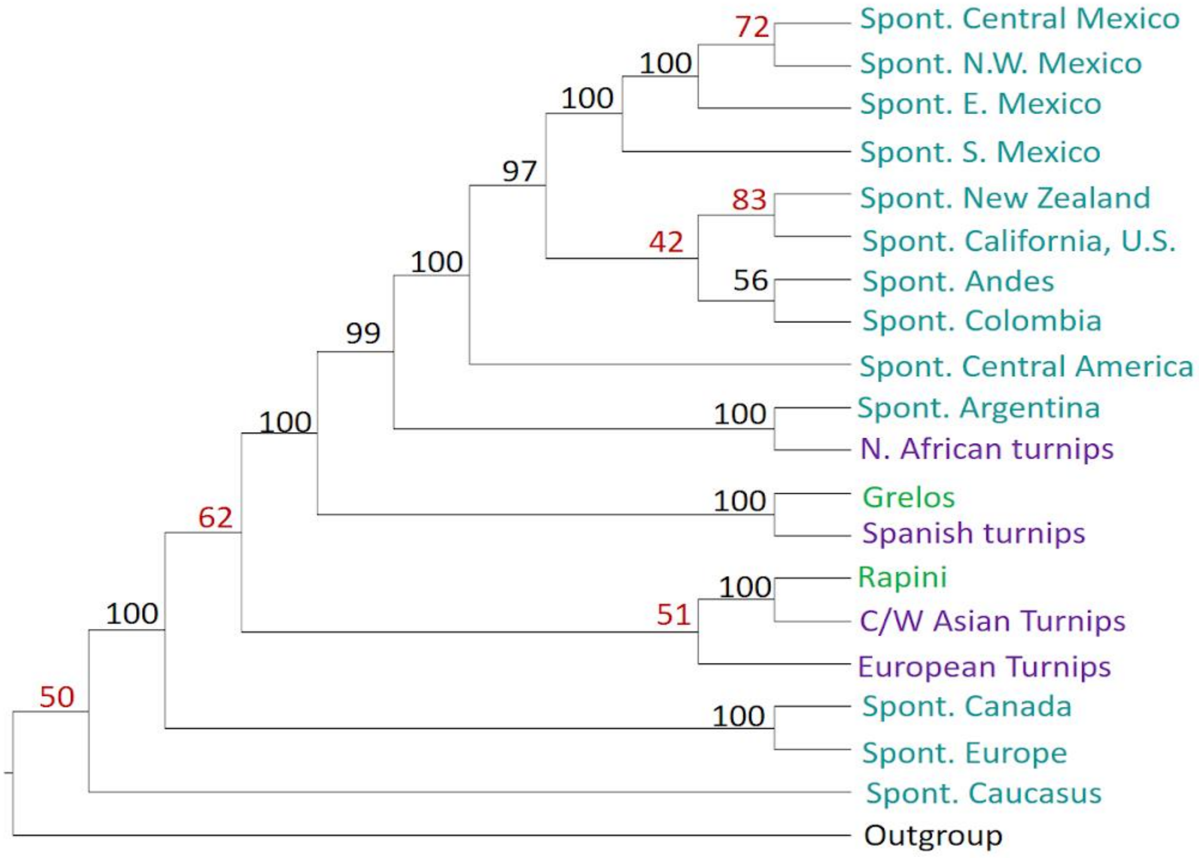


Figure 7. Coalescent tree from SVDquartets analysis. Spontaneously occurring samples are indicated in turquoise, turnips are indicated in purple, the outrgoup is indicated in black, and leafy crops are indicated in green.

Treemix indicated potential introgression from wild samples in the Caucasus to European weeds.

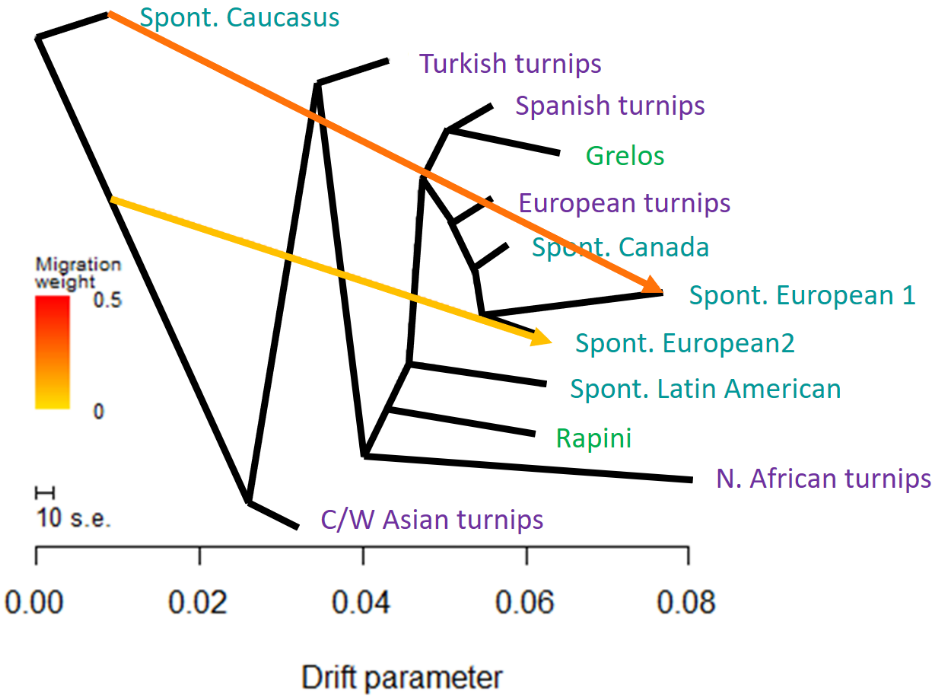


Figure 8. TreeMix diagrams with two migration edges. Arrows indicate vectors of introgression between groups. Turquiose text indicates spontaneously occurring populations, green text indicates leafy crops, and purple indicates turnip crops.

Niche modeling—Model C (Fig. 9), trained on 449 global occurrences, predicted a climatic niche fit with the Andes, southern and western Africa, southern Australia, a nearly continuous band between Anatolia and southwestern China, as well as much of North America, Europe, and New Zealand. The three models differed in terms of predicted ranges (Fig. 9, Supp. material 9) and the importance of bioclimatic variables in explaining occurrences (Table 2, Fig. 9). Model A (Supp. material 9), trained on Eurasian occurrences, predicted a relatively limited extent of *B. rapa* in Latin America focused on the Andes and southern South America but not in the central American and Mexican highlands. Temperature related variables (Bio1, Bio2, Bio4, Bio5, Bio9) were relatively important in constructing the model (Fig. 10) and the projected distribution favored cooler areas. Model B (Supp. material 9), trained on Latin American occurrences, relied more heavily on precipitation-related variables (e.g., Bio17, Bio18) and predicted a global distribution in relatively warmer areas. Omission rate on training samples was close to predicted omission for Eurasian, Latin American, Global occurrence data and the receiver operating characteristic curve (DeLong et al., 1988) showed an area under curve of 0.991, 0.985, 0.960 respectively, suggesting that the models fit the data reasonably well.

Figure 9. Model C: Species distribution models of spontaneously occurring *B. rapa* trained on 449 globally distributed occurrences.

Table 2. Top three environmental variables in order of relative contribution to each niche model. Isothermality is calculated as Mean Diurnal Range divided by Temperature Annual Range.

Model	**Variable**	**Percent contribution**	**Permutation importance**
Model A	Mean Diurnal Range of Temperature	36.2	45.5
	Precipitation Seasonality	17.3	0.6
	Annual Mean Temperature	11.3	2.4
Model B	Precipitation Seasonality (Coefficient of Variation)	29.6	3.7
	Isothermality	26.3	26.5
	Annual Mean Temperature	7.9	2.9
Model C.	Precipitation Seasonality	43.3	9.4
	Isothermality	13.7	9.3
	Precipitation of Driest Month	9.6	63.7

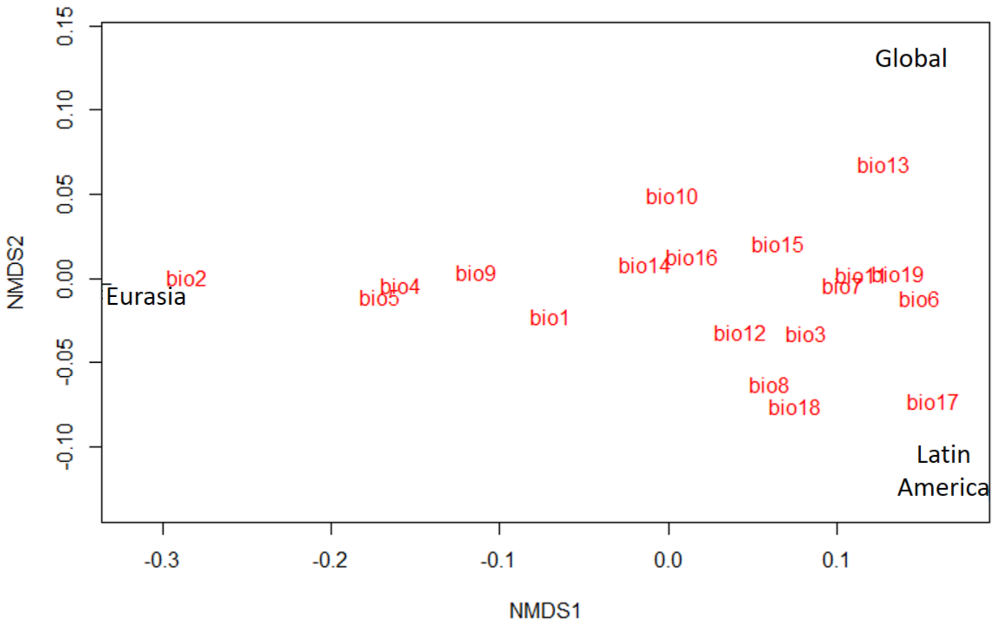


Figure 10. NMDS ordination indicating contribution of variables to each model. Bioclimatic variables (Bio1-Bio19) are explained in supplementary materials 3.

Discussion

***Dedomestication of Brassica rapa*—**Our results are consistent with McAlvay (Chapter 2) supporting a feral origin for weedy *B. rapa* in Europe, the Americas, and New Zealand, but also suggest exoferality via genetic contributions from wild populations in the case of European populations. European weeds had relatively high nucleotide diversity, countering expectations of a diversity bottleneck from domestication, and endoferal dedomestication. Contributions from wild relatives could have potentially replenished diversity in these populations. Admixture between wild Caucasian samples and feral *B. rapa* is evident in the fastSTRUCTURE plot, PCA, and TreeMix analyses of dataset A. Genetic differentiation between wild Caucasian samples and European weeds was also lower than that between Caucasian samples and European turnips. Admixture would also explain the inconsistent position of weedy European and Canadian samples in the SVDquartets coalescent analysis, which placed these groups as sister to all other crops and weeds in dataset A and nested within a clade of turnips in McAlvay (Chapter 2). Together, these results suggest a potential exoferal origin with contributions from wild populations as observed in beets (Sukopp et al., 2005) and radishes (Snow and Campbell, 2005). Adaptation to anthropogenic environments may pre-adapt crop populations to ferality (Hufbauer et al., 2012), and gene-flow from wild relatives may facilitate escape by imparting traits like seed dormancy and dehiscence that break the dependence of crop plants on humans (Gressel, 2005).

***Origin(s) of weedy Brassica rapa* populations outside of the native range**—Weedy populations of *B. rapa* from southern Quebec, Canada, are associated with European weeds and turnips in the fastSTRUCTURE, PCA, F_{ST}, and tree-based analyses and the Canadian weeds were most closely associated with weedy samples from the Netherlands in the neighbor-joining tree. Latin American weedy populations of *B. rapa* in Latin America form a cluster in the genetic structure and tree-based analyses. PCA, fastSTRUCTURE, and F_{ST} indices suggest that they are most closely associated with several groups, including European (especially Spanish) turnips, Central/West Asian turnips, European weeds, and North African turnips. The coalescent tree and fastSTRUCTURE plot showed an affiliation between Latin American weeds and North African turnips, which was corroborated by a close relationship between Argentinian samples and North African turnips in the PCA analysis. The association between Latin American weeds and Mediterranean crops (Spanish, Turkish, N. African turnips, and Rapini) evident in fastSTRUCTURE suggests a possible origin in the region, which would be consistent with the introduction of weedy forms with Spanish colonists as posited by Bye (1979) and Gade (1972). As we had no spontaneously occurring samples from Iberia or North Africa, this likely possibility has not been fully explored. Weedy field mustard is known to occur in North Africa (Fella, 2017), but is not present in Spain (Pers. comm, Pablo Velasco). Our single sample from New Zealand clustered with weedy *B. rapa* from Latin America in all analyses. Increased sampling in this region would lead to more robust inferences into the origins of these populations.

Spread within Latin America—Our fastSTRUCTURE analysis of dataset B, PCA of dataset B, coalescent tree, and neighbor-joining tree are consistent with an introduction into South America and/or Central America, with subsequent spread to California and Mexico. The fastSTRUCTURE plot supports an introduction into Central Mexico and spread to other parts of the country consistent with the hypothesis of Bye (1979) who suggested field mustard was introduced to Mexico as an agrestal in oats, and inadvertently spread to other parts of the country. The patterns of diversity are consistent with the spread of *B. rapa* from South America to Central America and California, and ultimate spread to Mexico with serial bottlenecks occurring due to founder effects.

Climatic niche model of *B. rapa*—The species distribution model for *B. rapa* trained on global occurrence data predicted suitable climate for spontaneous *B. rapa* in all continents but Antarctica, with especially high compatibility with temperate highland and coastal regions. The Eurasian distribution predicted was similar to the Eurasian mid-Holocene distribution model in McAlvay (Chapter 2), but with increased probability of fit in western Russia. The predicted Eurasian and North African distribution could be used to inform conservation and gap analysis of germplasm collections could guide collection of wild populations. The model indicated several areas of compatible habitat for weedy *B. rapa* where occurrence data has not been registered in the Global Biodiversity Information Facility (Supp. material 10) including Greenland and Eastern Africa. If *B. rapa* does not currently exist in these areas, they may be susceptible to invasion.

The climatic niches of *B. rapa* modeled based on Eurasian and Latin American samples differed in terms of variable importance, and projected global distribution. The model based on Eurasian occurrences favored cooler areas and had little overlap with the actual occurrence of *B. rapa* in Latin America. This model, however projected suitable habitat around southern Quebec, where the weedy Canadian samples that showed affinity for European weeds in the NJ tree, F_{ST} analysis, and PCA were collected. The model based on Latin American occurrences, favored warmer areas, and included little of Europe, where we found the *B. rapa* samples most closely related to Latin American populations in the tree-based analyses and fastSTRUCTURE analysis. A small area of southern Iberia, and parts of North Africa fit the model for suitable climate. Differentially modeled niches trained on samples from different parts of the world could be an artifact of phenotypic plasticity, enemy release (Gallagher et al., 2010), an underprediction of climate tolerance and therefore potential range due to unfilled habitats (Bocsi et al., 2016), or could suggest potential local adaptation. The latter possibility would require further study involving transplant experiments, selection scans, and/or other complimentary approaches. If populations of *B. rapa* are adapted to different temperature and precipitation regimes, they may harbor alleles useful for breeding *B. rapa* crops that impart resilience to abiotic stress.

***Consequences for management*—**While a diversity bottleneck is predicted from the founder effect (Allee 1931; Ellstrand and Elam 1993), a comparable amount of diversity exists between Latin American populations and closely related Eurasian and African populations, perhaps due to an exoferal origin. Though high levels of diversity do not appear to be essential to invasion success and rapid evolution in invasive species (Tsutsui et al., 2000), the substantial standing diversity in these populations could make them more readily adaptable to weed control methods and abiotic stresses (Sakai et al. 2001; Crawford and Whitney; 2010). Weedy *B. rapa* in Latin America may not be susceptible to the same herbivores and pathogens as most European *B. rapa* populations if they are adapted to different conditions. Our Species Distribution Models could be used to inform the control of field mustard as they indicate areas that are potentially vulnerable to invasion.

This study is the first to focus on the origins and spread of weedy *B. rapa* using genetic data. Future genetic studies incorporating wild material from around the Mediterranean may further clarify the origins of *B. rapa* in Latin America. This species, already a powerful study system for understanding diversification under human selection (Guo et al., 2014), has been identified as a promising candidate model organism for understanding the genomics of weediness and invasion (Basu et al., 2004). Future research could leverage the well annotated genome and short life-cycle of *B. rapa* for reciprocal transplant experiments and genomic studies of local adaptation.

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Chapter 4

Adopting and adapting: use and management of invasive field mustard (*Brassica rapa*) in Mexico

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"…When all is already withered

My little babies:

"Bread! Bread!" They cry to me

Just you [weedy field mustard], with your dew drops

clean the little faces of my babes

With your little green leaves,

Kindly you give us food…"

- Passage from Chawiyuyu Mama by Peruvian poet Ch'aska Anka Ninawaman in *Poesía en Quechua: Chaskaschay*. 2004. Abya-Yala. Passage translated from from Quechua to Spanish by Ch'aska Anka Ninawaman and from Spanish to English by Alex McAlvay

Abstract

Cultural reactions to biological invasions are not universally negative. While some cultures reject invasive biota, others embrace useful species and incorporate them into local subsistence practices. Since the introduction of weedy field mustard (*Brassica rapa*) into the Americas from Eurasia, at least two dozen indigenous groups from northwestern Mexico to southern Argentina have since adopted this plant as a food, medicine and/or animal fodder. To document the regional importance of this plant and potential for local practices to influence its evolution, we conducted interviews with members of eight cultural groups in Mexico. We found that use and management of *B. rapa* was patterned both by geographic proximity and linguistic affiliation between groups. We also found evidence for *B. rapa* cultivation and use declining in some areas. Encouragement of weedy field mustard in Mexico presents a powerful study system for ongoing domestication but

could also lead to conflicts between small-scale farmers who rely on the plant for food and conservation organizations and agronomic interests seeking to remove invasive plants.

Keywords: Ethnobotany, *Brassica rapa*, invasive species

Introduction

Ethnobotany has traditionally focused on the use of native plants by Indigenous peoples (dos Santos et al., 2014), and only recently have migrating plants and humans been the target of studies (Pieroni and Vandebroek 2008). Mounting evidence demonstrates that cultures do not universally reject invasive plants and in some cases exotic species may become important sources of foods, medicines, and materials (Blanckaert et al., 2007; Madamombe–Manduna et al., 2009; Dos Santos et al., 2014; Achigan–Dako et al., 2011). Although the use of newly encountered organisms is increasingly under investigation (Pieroni and Vandebroek, 2008), cases in which cultures actively encourage non-native plants are less well characterized. The study of human encouragement of exotic organisms provides the opportunity to understand how cultures incorporate newly encountered biota into their subsistence strategies and to anticipate potential conflicts between those propagating invasive plants for use and those seeking to remove them for ecological or agricultural reasons.

Field mustard (*Brassica rapa* L. Brassicaceae: 2n = 20), a weedy edible plant native to Eurasia, but widespread in the Americas, presents an interesting case of adoption of a non-native plant by diverse cultures over a large geographic area. In Eurasia, *B. rapa* was domesticated and selected for morphologically diverse crop forms (e.g., turnips, pak choi, napa cabbage, and oilseeds) making it a model of phenotypic diversification under artificial selection (Gómez-Campo and Prakash, 1999; Zhao et al., 2005; Guo et al., 2014; Warwick et al., 2008; Guo et al., 2014; Purugganan et al. 2000; Prakash et al. 2011, Prakash et al. 2009; McAlvay, Chapter 2). Weedy forms of *B. rapa*, possibly derived from feral European crops (McAlvay, Chapter 3), have become widespread agricultural weeds in temperate areas worldwide (Gressel, 2005). Weedy forms of *B. rapa* are widely distributed throughout the highlands of Latin America (GBIF.org [Accessed June 6, 2016]; Rios and Garcia, 1998; see McAlvay, Chapter 3). Historical accounts suggest that *B. rapa* may have arrived in the region during the early Spanish colonial period, but specific details surrounding the nature of the source population(s), timing, and number of introductions are unclear (Gade 1972; Bye 1979).

Following its introduction, weedy forms of *B. rapa* have been adopted as a food (e.g., Gade, 1972; Bye, 1979; Weismantel, 1989) condiment (Pennington, 1969), livestock forage (Vieyra-Odilon and Vibrans, 2001), birdseed (Linares and Aguirre, 1992), and medicine (Macía et al., 2005) (see Table 1 and Fig. 1). Different cultures favor the use of different plant organs such as root-hypocotyls and young leaves (Bye, 1979), mature leaves with or without inflorescences (Berlin et al., 1974; Gade, 1972; Weismantel, 1989), immature siliques (Linares and Aguirre, 1992) and mature seeds (Pennington, 1969). At least 23 different cultural groups in seven Latin American countries use field mustard in some manner (Table 1, Fig. 1). Field mustard is also used in U.S.A. and Canada by at least six cultural groups: the Xa’islak’ala, Kitasoo, Wuikinuxv (Compton, 1993) and Syilx (Turner et al, 1980) of the Pacific Northwest, Pomo of California (Chestnut, 1902), and Tsalagi of North Carolina (Witthoft, 1977).

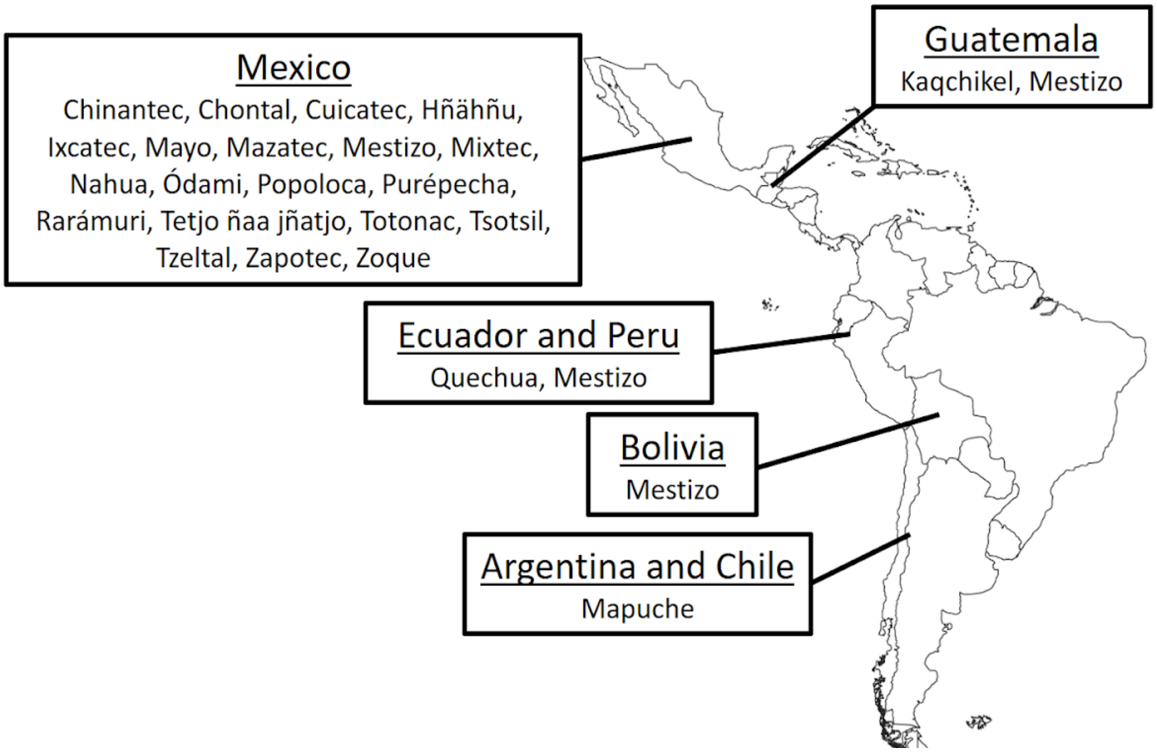


Figure 1. Map of Latin America indicating cultures that use spontaneously occurring *Brassica rapa*.

In some parts of Latin America, field mustard has become a substantial contributor to food security. Farfán et al., (2007) estimate 4.2 tons of *Brassica rapa* are consumed per year in a village of 2000 Tetjo Naa Jñatjo people, more than eight times more than the next most important weedy edible plant. Bye (1979) estimated that many Rarámuri people consume between 100-150 grams of fresh leaves per day for half of the year. In other cases, *B. rapa* is consumed much more occasionally, with an estimated 0.93kg consumed per year by Cuicatec people in the community of San Lorenzo Pápalo (Solis-Rojas, 2006). Yield by land area can be substantial (Bye 1979, Vieyra Odilon and Vibrans, 2001) and the sale of surplus *B. rapa* for food and fodder is an important income supplement in some regions (Vieyra-Odilon and Vibrans, 2001). Bye (1979) notes that it is especially key to Rarámuri subsistence because it is available at a time of year when other food is scarce. Field mustard is nutritious, with high levels of vitamin A, vitamin C, fiber, and iron (Munsell et al., 1953; Bye, 1979; Vieyra-Olidon and Vibrans, 2001).

To increase its accessibility and abundance, several cultures engage in some form of encouragement of field mustard. Management techniques include intentional sparing of spontaneously-occurring *B. rapa* while weeding (Weismantel, 1989; Gade, 1972; Vieyra-Odilon and Vibrans, 2001), and sowing seeds in plots (Bye 1979; Pennington, 1969; Solís and Estrada, 2014; Blancas et al., 2013). The Rarámuri tradition of cultivating *B. rapa* was described as early as 1776 (Bye, 1979), suggesting an early adoption of this plant into local subsistence. Field mustard has been independently identified as potentially undergoing ongoing domestication in several parts of Latin America. Gade (1972) and Bye (1979) suggest that cultivation of weedy field mustard in Peru and Mexico respectively represent powerful contemporary study systems for understanding domestication as it occurs. Barreau (2016) suggests that field mustard used by the Mapuche of Argentina is semi-domesticated.

Local names for field mustard throughout Latin America are varied (Table 2). The Spanish terms nabo and/or mostaza are used broadly along with various indigenous names, some apparently an adaptation of the Spanish term (e.g., the Mayo word *mastaza* or Tzotzil word *napux*), and others related to similar local flora (e.g., the Rarámuri term *mekuásari*, which is related to words for other members of Brassicaceae in the language [Bye, 1979]). Various cultures recognize and name distinct morphotypes. For example, Tzeltal (Berlin et al., 1974), and Nahua (Blancas et al., 2013) differentiate between a smooth-leaved form (Nahua: *colesh*; Tzeltal: *caxlan napush*) and a less desirable pubescent form (Nahua: *coleshtenaztli*; Tzeltal: *ch'ix napush*). To investigate linguistic patterns that may be associated with the spread of field mustard, we constructed a map of 23 local Spanish and indigenous names of *B. rapa* throughout Mexico using the *Banco de Información Etnobotánica de Plantas Mexicanas* (BADEPLAM).

Table 1. Ethnobotanical use and names of *B. rapa* in Latin America. lv=leaves, fl=inflorescence, rt=root-hypocotyl, sd=seeds. fd=food, fr=fodder for livestock or birds, md=medicine.

Country	Culture/Location	Local name(s)	Part used	Use type	Source
Argentina	Bariloche, Argentina		lv	fd	Rapaport and Ladio, 1999
	Mapuche/Argentina/Chile	repollo del campo, repollo silvestre, napor	lv	fd	Ladio, 2001
	Mapuche/Chile	yuyo	lv	fd, md	Barreau, 2014
	Neuquén, Argentina		lv	fd, md	Ladio, 2005
Bolivia	La Paz, Bolivia	mostaza	lv, fl, st	md	Macia et al., 2005
Ecuador	Quito, Ecuador	hojas de nabo	lv	fd	Munsell, et al., 1953
	Ecuador/Peru	ñabos, nabo silvestre o yuyo	fl and lv	fd	Mikuy and Mikuy, 2010
Guatemala	Guatemala		lv	fd	Munsell et al., 1950
	San Andres, Guatemala			md	Comerford, 1996
Mexico	Chinanteco/Oaxaca, Mexico	? ma. how		fd	Lipp, 1971
	Chontal/Mexico		st	md	Magaña-Alejandro, 2009
	Cuicateco/Oaxaca, Mexico	jiun duc iyá	lv	fd	Solis-Rojas, 2006
	Distrito Federal, Mexico	flor de pájaro, nabo	lv	fr, fd, md	Azcarraga-Rosette, 2004
	Estado de México, Mexico	nabo, vaina	sd, lv, st, fl	fd, fr	Vieyra-Odilon and Vibrans, 2001
	Estado de México, Mexico	alpiste	br	fr	Albarrán-Mondragón, 2009
	Estado de México, Mexico	nabo		fr	Chávez-Mejía, 1998
	Hidalgo, Mexico	nabo	fl	fr	Zamora-Martínez and Barquín-López, 1997
	Ixcateco/Oaxaca, Mexico	cilandrillo	lv, st, fl	md, fr	Rangel-Landa and Lemus, 2002
	Maya/Quintana Roo, Mexico	repollo, col,	lv	fd	Anderson et al., 2005
	Mayo/Mexico		sd	md	Salazar-Márquez, 1997
	Mayo/Sinaloa, Mexico	mastaza,	sd	md	Marquez-Salazar, 1997
	Mazahua/Mexico			fd	Farfán et al., 2007
	Mexico	nabo, quelite de agua		fd	Basurto-Peña, 2011
	Michoacán, Mexico	nabo	rt, lv	fd	Loredo-Medina, 2000
	Mixteco/Guerrero, Mexico	mostaza	lv, st, fl	fd	Viveros and Casas, 1985
	Mixteco/Guerrero, Mexico	mostaza, yiua calishi	lv, st, fl	fd, fr	Casas et al., 1994
	Mixteco/Mexico		lv, st, fl	fd	Casas and Viveros, 1994
	Morelos, Mexico	mostaza	lv, st, fl	md	Monray-Ortiz and Castillo-España, 2000
	Morelos, Mexico	mostaza	lv, st, fl	md	Gómez and Chong, 1985
	Cuicatec, Popoloca, Mazatec			fd	Casas et al., 2010
	Nahua/Hidalgo, Mexico	apox, nabo fino	br	fd	Villa-Kamel, 1991
	Otomí/Estado de México, Mexico	mostaza	br	md	Camacho, 1985
	Puebla, Mexico	quelite nabo, nabosquilit	lv	fd	Basurto-Peña et al., 1998
	Puebla, Mexico	nabo		md, fd	Rodríguez-Acosta et al., 2010
	Puebla, Mexico	col, kolix, nda kujlú	lv	fd	Mota-Cruz, 2007
	Puebla, Mexico	yiwa calishi, nabo, mostaza	lv, br	fr, fd	Casas et al., 2001
	Purépecha/Mexico			fd	Caballero and Mapes, 1985
	Purépecha/Michoacán, Mexico	mortanza, nabo, nipohikun, nipajip'kun mortanza, xakua mortanza	lv, st, fl	fd, fr, md	Caballero and Mapes, 1982
	Raramuri/Mexico		lv	fd	Larouchelle and Berkes 2003
	Tarahumara/Chihuahua, Mexico	guiliba a'lasini	lv, st, fl	fd	Mares-Trias, 1982
	Tarahumara/Chihuahua, Mexico	mokasari,	lv	fd	Pennington, 1963
	Tarahumara/Chihuahua, Mexico	acelga, quelite, mostaza	lv	fd	Camou-Guerrero, 2008
	Tepehuano/Chihuahua, Mexico	mostaza	sd, lv, st, fl	fd, md	Pennington, 1969
	Tlaxcala, Mexico	nabo		fd, fr	Vibrans, 1997
	Totonaco/Puebla, Mexico	nabo	br	fd	Castro-Lara, 2000
	Tzeltal/Chiapas, Mexico	nabos	lv, fl	fd	Berlin et al., 1974
	Tzotzil/Chiapas, Mexico	jolinom napux, juljul nabo, kaxlan napux, batz'i napux, ch'ix napux	rt, lv	fd	Breedlove and Laughlin, 1993
	Yucatán, Mexico	colinabo	rt, lv	fd	Sousa-Novelo, 1950
	Zapotec/Mexico		lv	fd, md, sp	Hunn, 2008
	Zoque/Chiapas, Mexico	nabo		fd	Isidro-Vázquez, 1997
Peru	Chincero, Peru		lv	fd	Franquemont, 1990
	Vilcanota, Peru		lv	fd, fr	Gade, 1975

To understand cultural and geographic differences in the ethnobotany of *B. rapa* across cultures, AM conducted interviews and surveys with members of eight cultural groups in Mexico. Mexico was selected because it is in one of the world's primary domestication centers (Vavilov, 1951; Harlan, 1975), is a center of cultural diversity (MacNeish, 1992), and past work has suggested the potential for ongoing domestication of *B. rapa*. In addition, certain contemporary traditional management regimes in Mexico have been shown to be responsible for domestication-like divergence between managed and wild populations (Casas et al., 2007; Blanckaert 2013). Specifically, we used semi-structured interviews and surveys to characterize local management, preferences, and knowledge surrounding *B. rapa* in Tzotzil, Tzeltal, Rarámuri, Nahua, Hñähñu, Mestizo, and Tetjo Naa Jñatjo communities. We analyzed yes/no survey response data surrounding use, management, and preferences for *B. rapa* with a clustering analysis to visualize similarities and differences across cultures. Clustering analyses have been used effectively in past comparative ethnobotanical studies (Georgian and Emshwiller, 2013). Using the interview data, we aim to address the following questions: 1) How do the uses, preparations, and preferences surrounding *B. rapa* vary across cultures? 2) Does use and management of *B. rapa* follow geographic and/or linguistic patterns? 3) How is *B. rapa* managed throughout Mexico and do any practices mentioned have the potential to influence the evolution of managed populations? 4) Do local names for *B. rapa* follow geographic patterns in Mexico?

Materials and Methods

***Study sites*—**This research was undertaken with along a Northwest-Southeast transect of Mexico spanning 29 communities, six states, eight cultural groups, and four major language families (Fig. 2, Table 3.).

Figure 2. Interview locations and ethnic groups. Map data: 2018 Google, INEGI

Table 3. Locations and ethnic groups of interviewees.

Ethnic group	Language family	Mexican State	Communities
Hñähñu	Oto-Manguean	Hidalgo	Ixmiquilpan
Zapotec	Oto-Manguean	Oaxaca	Oaxaca City, Ixtlán de Juárez, Evangelista Analco
Tetjo ñaa jñatjo	Oto-Manguean	State of Mexico	Río Hoyo Buenavista, San Felipe del Progreso
Tzotzil	Maya	Chiapas	San Cristobal de las Casas, Zinacantán, Chamula, San Andrés Larráinzar
Tzeltal	Maya	Chiapas	San Cristobal de las Casas, Amatenango del Valle
Mestizo	Indo-European	State of Mexico	Mexico City, Santa María Jajalpa, Toluca, Santiago Tianguistenco, Ozumba, Texcoco
Rarámuri	Uto-Aztecan	Chihuahua	Creel, Bahuinocachi, Rancho Blanco, Norogachi, Gumisachi, Choguita, Cocherare, Panalachi, Rejogochi, San Ignacio
Nahua	Uto-Aztecan	Veracruz	Soledad Atzompa

Fieldwork—Fieldwork was conducted over 4.5 months spanning 5 trips, Summer 2014, Summer 2015, Winter 2015-2016, Spring 2016, and Summer 2016. All interviews were conducted with approval from University of Wisconsin-Madison's Social and Behavioral Science Institutional

Review Board (#2014-0828 #IRB00022321; #2015-0666-CP001). Interviews were conducted in Spanish and adhered to International Society for Ethnobiology standards including prior informed consent. Voucher specimens of field mustard were collected and deposited in the National Herbarium of the National Autonomous University of Mexico (MEXU), and Wisconsin State Herbarium (WIS) at the University of Wisconsin-Madison.

Structured surveys—AM administered 46 surveys with 14 yes/no questions to interviewees. The survey questions can be found in supplementary materials 6. Survey data was analyzed using non-metric multidimensional scaling (NMDS) executed in the R package “vegan” to better understand relationships between cultures and their use and management of *B. rapa*. NMDS was chosen as it does not attempt to maximize variance or correspondence of different objects. Responses of all respondents from each culture were fit to the ordination using the envfit command in the vegan.

***Semi-structured interviews*—**AM conducted 138 semi-structured interviews and two focus groups across 29 communities. Individuals were selected from each community through snowball sampling and included farmers and market vendors. Semi-structured interviews were conducted surrounding three main topics: (1) usage: e.g., parts used, preparation, preservation, frequency of use, (2) production and management: e.g., spatial context, productivity, recognized morphological variation, community rules surrounding resource extraction, management type emphasizing possible artificial selection, source for seeds, cropping of associated plants, and economic value and (3) traditional ecological knowledge: e.g., distribution and abundance, phenology, songs and stories, nomenclature, interspecific interactions, and similar plants. Example semi-structured interview questions can be seen in supplementary materials 7.

***Distribution of local names for field mustard*—**Geographic patterning of local names for plants can provide information about the introduction and spread of plants and uses for plants (Roullier et al., 2013). Many local and Indigenous names for *B. rapa* throughout Mexico are derived from the Spanish word for turnip, *nabo,* or the Spanish word for mustard, *mostaza*. To investigate the spatial distribution of common names for weedy *B. rapa* across Mexico, we collected and mapped 23 local words for field mustard in Indigenous and non-Indigenous languages, classified the names as derived from *nabo* or *mostaza*, and drew hulls around geographic clusters of the two categories.

Results

Structured surveys

The NMDS analysis (Fig. 3) indicated relatively cohesive clustering of Rarámuri and Nahua respondents' answers within cultural groups, and these two cultures were most similar to each other. Tzotzil and Tzeltal responses clustered with each other but did not form discrete groups separating these two Mayan linguistic groups. Zapotec responses were similar to those of the Tetjo Naa Jñatjo respondents, and responses from Mestizo individuals were the most diverse, but were generally similar to Zapotec and Tetjo Naa Jñatjo, or Hñähñu responses. Correlations between survey questions and the NMDS axes (Table 4) indicate that use for birdseed, commercialization, fertilization, and seed exchange were associated with Oto-Manguean-speaking (Zapotec, Tetjo Naa Jñatjo, and Hñähñu) and Mestizo responses. Use of young leaves and roots and collection of spontaneously occurring plants were associated with Uto-Aztecan-speaking (Nahua, Rarámuri) and Mayan-speaking (Tzotzil, and Tzeltal) responses. Use of mature leaves and flowering tops was associated with Oto-Manguean-speaking (Tetjo Naa Jñatjo and Zapotec) responses. The drying of leaves, and medicinal use were associated with Uto-Aztecan-speaking groups: the Nahua and Rarámuri.

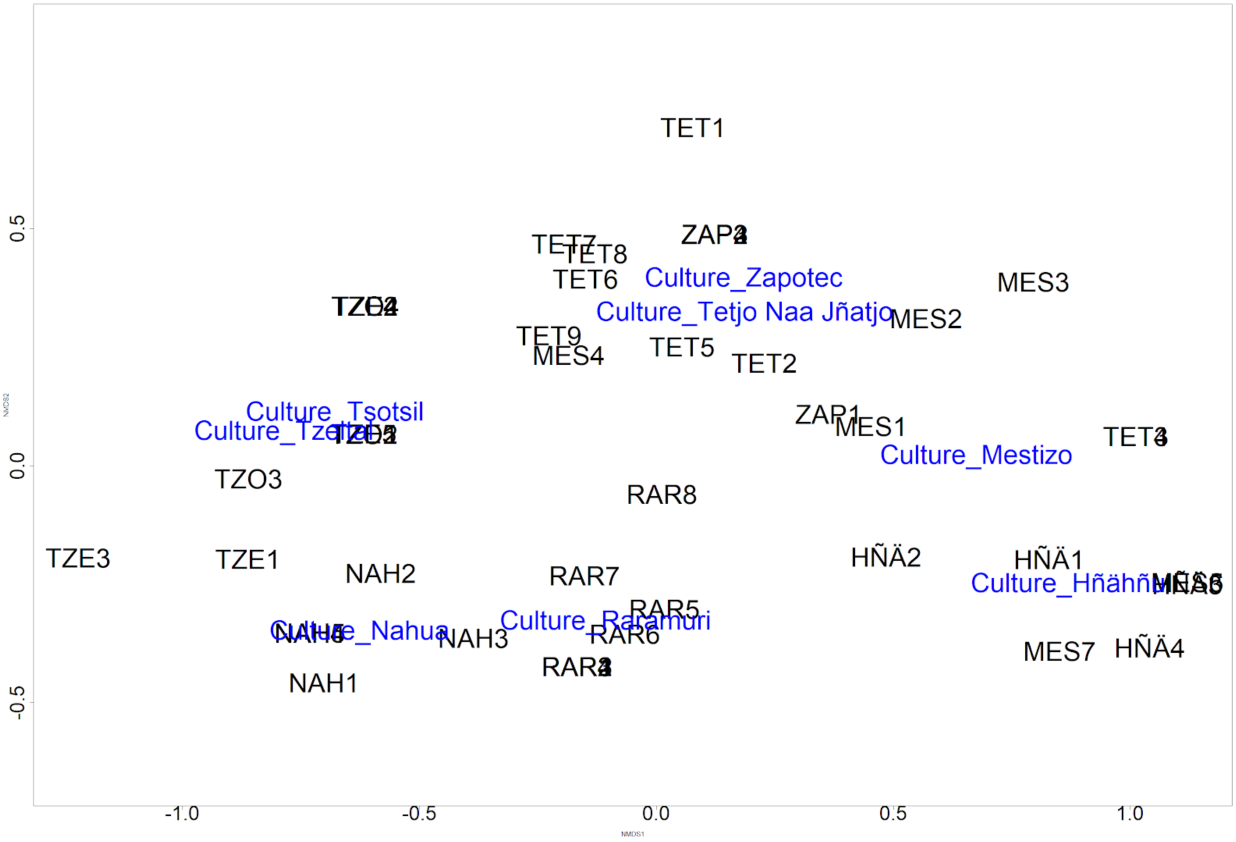


Figure 3. Non-metric dimensional scaling of survey responses from 45 individuals representing 7 ethnic groups. Black text indicates individual responses from respondents. Cultural groups are indicated with the following codes: Tzotzil (TZO), Tzeltal (TZE), Rarámuri (RAR), Nahua (NAH), Hñähñu (HÑÄ), Mestizo (MES), and Tetjo Naa Jñatjo (TET), followed by an anonymized respondent code. Blue text indicates cultures fit to the ordination using the envfit command in R.

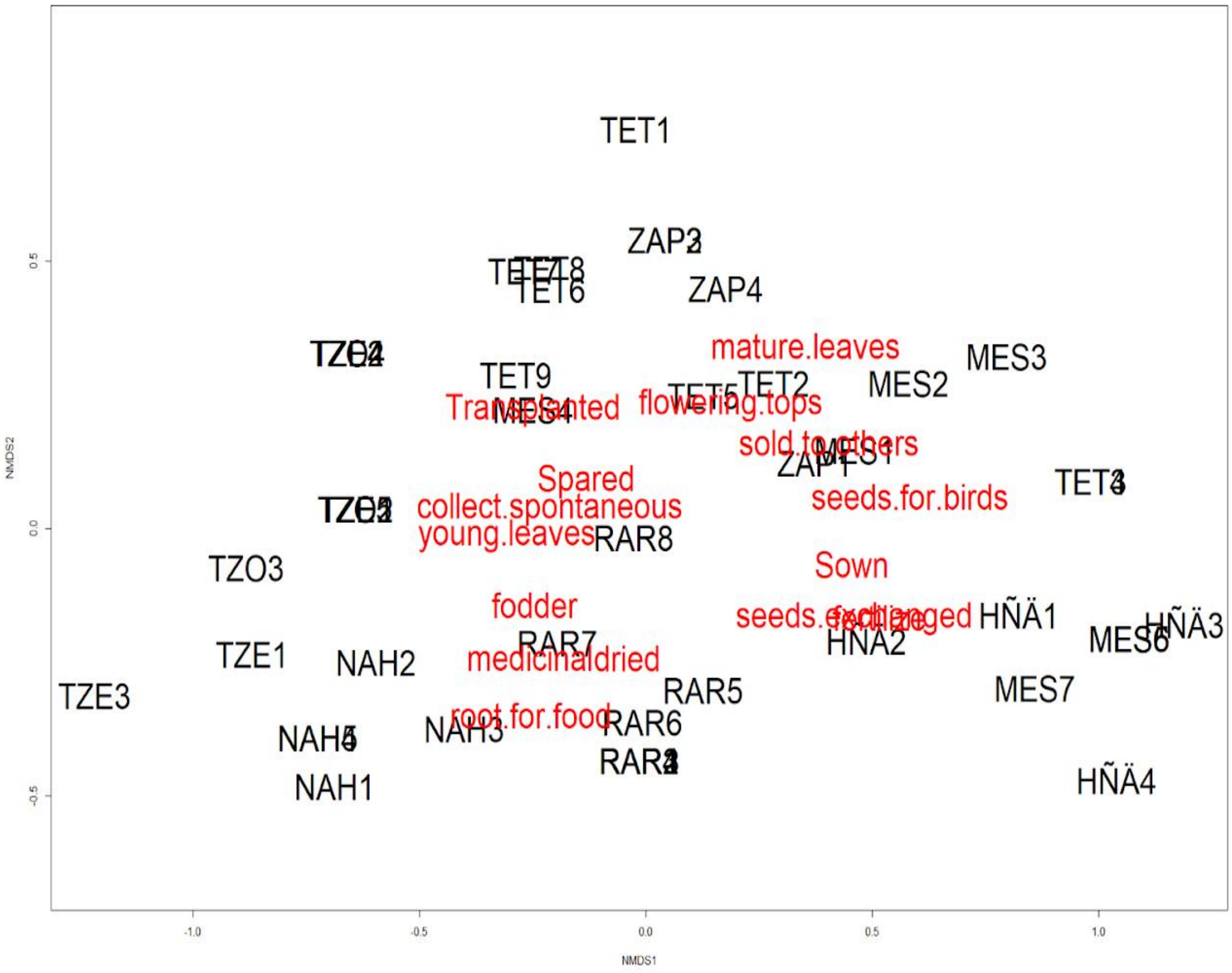
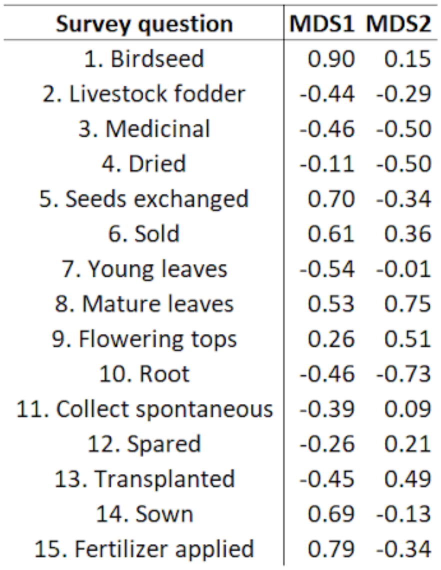


Figure 4. Correlations between survey question and NMDS positions.

Table 4. Correlations between survey questions and positions on NMDS.



Survey question	MDS1	MDS2
1. Birdseed	0.90	0.15
2. Livestock fodder	-0.44	-0.29
3. Medicinal	-0.46	-0.50
4. Dried	-0.11	-0.50
5. Seeds exchanged	0.70	-0.34
6. Sold	0.61	0.36
7. Young leaves	-0.54	-0.01
8. Mature leaves	0.53	0.75
9. Flowering tops	0.26	0.51
10. Root	-0.46	-0.73
11. Collect spontaneous	-0.39	0.09
12. Spared	-0.26	0.21
13. Transplanted	-0.45	0.49
14. Sown	0.69	-0.13
15. Fertilizer applied	0.79	-0.34

Semi-structured interviews

Use, management, and parts used of field mustard varied substantially across cultural groups (Table 5). Members of all cultures reported using leaves of the plants for food, and all but Hñähñu respondents reported harvesting spontaneously occurring plants. Five out of eight groups collected and sowed seed of field mustard. Many communities of different cultures around Mexico City reported growing *B. rapa* commercially as birdseed. Rarámuri, Mestizo, and Tetjo Naa Jñatjo respondents reported decreased use of *B. rapa* in recent years.

Table 5. Names, management practices, parts used, uses, exchange, and commerce of *B. rapa* across 8 different Mexican cultural groups. Tol=spared/tolerated when weeding, sow=seeds sown, tra=transplanted. Lv=leaves, fl=inflorescence, rt=root-hypocotyl, sd=seeds. Fd=food, fr=fodder for livestock or birds, md=medicine.

Culture/Location	Local name	Management	Part used	Use type	Seeds exchanged	Sold
Tzotzil/Chiapas	napux	tol	lv	fd, fr	no	no
Tzeltal/Chiapas	nabos	tol	lv	fd, fr	no	no
Rarámuri/Chihuahua	mekuásari	sow, tol	lv, fl, rt	fd, fr	yes	no
Nahua/Veracruz	quilapox, apox quilitl	tol	lv, rt	fd, fr, md	no	no
Hñähñu/Hidalgo	nabo, vaina	sow, tol	lv, fr	fd, fr	yes	yes
Mestizo/State of Mexico	nabo, nabitos, vaina	sow, tol, tra	lv, rt, fl, sd	fd, fr	yes	yes
Tetjo Naa Jñatjo/State of Mexico	mʉbʉ, corazones	sow, tol	lv, fl	fd	yes	yes
Zapotec/Oaxaca	mostaza	sow, tol	lv, fl	fd, fr	yes	yes

Tzotzil and Tzeltal**—**Tzotzil and Tzeltal respondents reported similar practices. Both groups occasionally harvest spontaneously occurring *B. rapa* in their fields. Some Tzotzil interviewees mentioned growing B. *rapa* from seed in plots of recently removed livestock corrals or in homegardens. Respondents of both groups mentioned purchasing seed from local markets. Almost all of the bundles of leaves sold as *nabos* (Tze.) or *napux* (Tzo.) in markets were *Brassica napus*. Tzotzil individuals distinguished between “wild” (*B. rapa*) and “Castillian” (*B. napus*) *napux*.

Rarámuri**—**Rarámuri interviewees mentioned scattering seeds directly in tilled livestock manure in areas where sheep, goat, or cow corrals had been recently removed. Seeds for sowing are harvested from both spontaneous and previously planted individuals but are preferentially collected from large plants with large fruits. One respondent reported sowing field mustard in a relay intercrop system before other crops were finished producing. Spontaneously occurring *B. rapa* was frequently associated with oat fields and less commonly harvested than sown populations. Most respondents preferred to consume very young plants with large, non-bitter leaves and crisp hypocotyls, though some individuals reported repeatedly harvesting immature inflorescences from mature plants. After harvesting, plants are frequently rubbed between the palms of the hands and dried over the hearth or on tin roofs to make dried field mustard *(quelite pasado*) for future use. One interviewee mentioned that *quelite pasado* is an important food at the religious feasts during holy week (*Semana Santa*). Many people commented that *mekuásari* “does not tire,” and the greens are a reliable source of food when other nourishment is scarce. Several respondents reported a decline in the tradition of sowing *B. rapa* in plots. Among the reasons cited were engaging in paid agricultural labor like apple picking during the cultivation season of *B. rapa*, and a recent drought which forced many Rarámuri to sell or eat their livestock, leading to a shortage of manure-rich plots. Many respondents mentioned that a new brassicaceous weed (*Raphanus raphanistrum*: wild radish) that looks like *B. rapa* when young but tastes unpleasant, has arrived in the last ten years with oat and weed seed from Central Mexico.

***Nahua*—**Nahua interviewees from the village of Soledad Atzompa mentioned mainly using spontaneously occurring *B. rapa*, but several people mentioned intentionally sparing small stands of prolific individuals when weeding to encourage self-seeding of a field. In a focus group, one person mentioned that if you did not have *B. rapa* in your field, you could hypothetically ask a neighbor to collect some seeds for you, though others mentioned that this was not a common practice. One respondent mentioned that a tea of the *B. rapa* root-hypocotyl mixed with *ruda* (*Ruta graveolens*) can be used to stimulate appetite in children. This plant is widely used as fodder for rabbits, goats, chickens, and sheep, and while not used a birdseed, interviewees noted that wild birds are attracted to the seeds. Field mustard in this area is often eaten raw, boiled, or fried with egg and/or salsa verde.

***Hñähñu*—**Hñähñu respondents grew *Brassica napus* extensively for sale of birdseed to Central Mexican markets and only rarely used *B. rapa*. One interviewee mentioned harvesting leaves from spontaneously occurring *B. rapa* to sell when working in commercial lettuce fields. Use of the young leaves for food was not popular in the area.

Mestizo—Mestizo interviewees in the State of Mexico reported diverse use and management practices. Leaves, flowering tops, and infructescence of *B. rapa* and *B. napus* were widely sold in the markets of Mexico City, though many vendors mentioned less *B. rapa* and more *B. napus* being sold in recent years. This trend was apparent in the span of three years during which fieldwork was conducted. The final year, it was difficult to find any *B. rapa* being sold. In Ozumba, *B. rapa* was grown in mixed plots of *B. rapa* and *B. napus* for birdseed. Leaves and flowering tops are eaten raw in salad with lime, 99autéed, or boiled. At the Ozumba market, seed was sold as *criollo* (*B. rapa*) or *Canadiense/canola* (*B. napus*). Around Ozumba, *B. rapa* leaves were often prepared *capeado*, or battered in egg whites and fried, a popular preparation for other local vegetables. In the small town of Santa María Jajalpa, interviewees mentioned transplanting young *B. rapa* to new locations to spare them from weeding and sowing seeds from the largest, most robust spontaneously occurring plants. Mestizos interviewed in Texcoco grew *B. rapa* on industrial farms for its edible leaves, flowering tops, and seeds. One agricultural extension worker mentioned the noxious nature of weedy *B. rapa* and said that he recommended that farmers remove it with pesticides.

Tetjo Naa Jñatjo—Tetjo Naa Jñatjo reported growing *B. rapa* in greenhouses for leaves and inflorescences. Many individuals commented that *B. rapa* inflorescences were their favorite vegetable. Tetjo Naa Jñatjo reported that use of spontaneously occurring *B. rapa* was declining because of more industrialized agriculture. Since many farmers in these communities work various jobs in Mexico City for five days a week, available time to farm is limited and herbicides have been implemented to save time.

Zapotec—Zapotec respondents mentioned extensive harvest of spontaneously occurring *B. rapa* in fields and occasionally collecting and sowing seed in cash crop fields of peas, radishes, cilantro to augment local *B. rapa* populations.

Distribution of local names for field mustard**—**We found spatial patterning of words for field mustard across Mexico, with words derived from *mostaza* tending to occur in the Sierra Madre Occidental mountains of western Mexico, south and west of Mexico City, and in the northern Highlands of Oaxaca. Words derived from *nabo* are used in the eastern Transverse Neovolcanic Axis and into northwest Chiapas.

Figure 5. Map of names for field mustard throughout Mexico related to the Spanish words *mostaza* and *nabo*. Of the 23 names surveyed, 10 examples demonstrating the patterns are shown. Red text indicates names likely derived from the Spanish word *mostaza* or mustard. Blue text indicates names likely derived from the Spanish word *nabo* or turnip.

Discussion

Geographic and language-family patterns**—**The NMDS analysis indicated that very close associations between responses from respondents of ethnic groups in the same language family despite varying geographic distances between groups. This held true for not only the Maya-speaking Tzotzil and Tzeltal communities which are geographically proximate (in the same or neighboring municipalities), but also for the Uto-Aztecan-speaking Nahua and Rarámuri communities, which are more than 1400 km apart. Zapotec and Tetjo Naa Jñatjo responses were similar despite communities being more than 450 km away. Hñähñu responses were more closely associated with Mestizo responses than with other Oto-Manguean speakers, though all of the Oto-Manguean groups all clustered toward intermediate or higher values of NMDS1. The association of Oto-Manguean respondents with Mestizos may be because the Hñähñu, Zapotec, Tetjo Naa Jñatjo, and Mestizos interviewed were all either in the State of Mexico or adjacent states. Hñähñu individuals also reported being involved in growth and sale of *B. rapa* for birdseed to the State of Mexico, where the Mestizos who were interviewed were located. The long-distance similarity between related cultural groups in terms of adoption of an exotic weed suggests that how a culture decides to interact with a newly-encountered plant is not completely dictated by learning its use from geographical neighbors. While language-family is not a proxy for cultural similarity, cultures in the same language-family may have shared cultural features that incline them to interact with new flora in a particular manner. We found that local names for weedy field mustard derived from the Spanish words for turnip and mustard were separated geographically. This may suggest separate introductions of *B. rapa* into Mexico or differences in phenotypes or uses for *B. rapa* in different regions.

Changing traditions and loss of knowledge—Acculturation and other forces can threaten traditional plant knowledge, (Gandolfo and Hanazaki 2014; Reyes-García et al. 2007; Voeks and Leony 2004), but some researchers have found that plant knowledge can be resilient over time and in the face of globalizing forces (Zarger and Stepp 2004; Müller-Schwarze 2006; Mathez-Stiefel et al. 2012; Furusawa 2009; Vandebroek and Balick 2012). Bye (1979) suggests that cultivation of *B. rapa* has largely replaced similar practices to encourage the native edible plant *Lepidium virginicum*, and it appears that in several areas of Mexico *B. napus* has partly replaced *B. rapa* as a food and fodder crop. This trend of reduced use of *B. rapa* is also noted by

Barreau (2016) among the Mapuche of Argentina and Greenberg (2015) with Tzotzil and Tzeltal individuals in Mexico. Greenberg (2015) found that many peri-urban adults expressed that while they enjoyed field mustard, their children did not. In Ecuador, field mustard is considered a low-status food in several communities and its use discouraged in favor of higher-status refined foods (Weismantel, 1989). The case of field mustard in Mexico provides an example of an exotic plant that has been adopted by diverse cultures leading to new traditions of use, management, and preparation, but is now declining in popularity in some regions due to more recently introduced plants and changing livelihoods. This example shows traditional knowledge not as a static corpus of knowledge, but as dynamic and quick to adapt to changing conditions (Madeiros, 2013). In general, the mechanization of agriculture and use of herbicides in Mexico threatens weedy edible plants as a traditional food source (Blanckaert et al., 2007).

Encouragement of an invasive species—Field mustard can compete with crop plants (Basu et al., 2004) and the Mexican government recognizes field mustard as an invasive plant (Vibrans, 2002) for which it has a policy of removal (Comité Asesor Nacional sobre Especies Invasoras, 2010). This could potentially lead to conflict with small-scale farmers who depend on this plant as a food resource, especially since most cultural groups interviewed engaged in some form of management to promote the abundance of weedy *B. rapa*. This potential issue could also take place across Latin America as a whole, where it is used by at least 24 cultures from northwestern Mexico to Argentina (e.g., Gade, 1972; Berlin et al., 1974; Bye, 1979; Ladio, 2001; Vieyra-Odilon and Vibrans, 2001; Farfán et al., 2007).

Potential model system for ongoing domestication—The extensive management of *B. rapa* throughout Mexico provides an opportunity to investigate ecological, cultural, and genetic factors involved in bringing wild plants under cultivation. As different cultures engage in distinct management activities (tolerating, transplanting, sowing), countrywide genetic studies could reveal the strength of selection of these respective practices. Additionally, the diversity of preferences for different plant organs (leaves, root-hypocotyls, flowers, infructescences, inflorescences) provides and interesting parallel with the morphologically diverse *B. rapa* crops of Eurasia.

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Chapter 5

Genetic and phenotypic consequences of Indigenous management of feral *Brassica rapa* in Mexico.

Alex C. McAlvay, Robert Bye, Eve Emshwiller

Abstract

Understanding the process of reciprocal genetic and cultural change involved in the domestication process has long been a focus of archaeology, genetics, and numerous other fields. Unfortunately, it is difficult to make inferences about the complex ecological, cultural, and evolutionary factors involved in domestication processes that happened thousands of years ago. Spontaneously occurring populations of field mustard (*Brassica rapa*) in Northwest Mexico provide an opportunity to study this process in real-time. We collected field mustard samples from populations cultivated by Rarámuri farmers and unmanaged populations in Chihuahua, Mexico for phenotypic and population genomic analysis. We found significant differences in flowering time and between managed and unmanaged populations and genetic differentiation of two managed populations from unmanaged populations in the same communities. This genomically-enabled short-generation plant could provide a powerful study system in the future for further understanding the ecological and cultural aspects of domestication.

Keywords: Domestication, contemporary evolution, incipient domestication, traditional resource management

Introduction

Domestication is driven by a complex mix of ecological, biological, and cultural factors (Price et al., 2011; Gepts et al., 2012). Understanding the process of reciprocal genetic and cultural change involved in the domestication process has long been a focus of archaeology, genetics, linguistics, and other disciplines (Meyer and Purugganan, 2013; Zeder, 2015). Domestication research provides insight into the nature of both contemporary crop genetic resources (Harris, 2012; Zeder, 2015) and evolutionary processes in general (e.g., Darwin, 1868; Andersson and Georges, 2004; Ross-Ibarra et al., 2007; Meyer and Purugganan, 2013). Research on domestication has focused on selection processes often taking place thousands of years ago (Larson et al., 2014), in cases where it has been difficult to empirically characterize the ecological context and human practices involved (Parker et al., 2014; Zeder, 2015).

To circumvent this difficulty, some researchers have turned to contemporary study systems in which humans manage otherwise wild plant populations by weeding, saving and sowing seeds, transplanting, or other activities (Gade, 1972; Bye, 1979; Casas et al., 2007; Elias et al., 2007; Hughes et al., 2007; Blanckaert, 2011). Many of these studies have focused on non-model and long-lived organisms such as cacti (e.g., Casas et al., 1997, 1999; Rodríguez-Arévalo 2006; Parra, 2008) and leguminous trees (Zárate et al., 2005) that can limit genomic and transplant experiments. Most of this research has also focused on native plant species which have coexisted with local cultures for an unknown period of time (e.g., Casas et al., 2007; Aguirre-Dugua et al., 2012), making the time depth of management unclear.

Field mustard (*Brassica rapa* L.) managed by Indigenous farmers presents a powerful study system to study ongoing evolution under human management (Gade, 1972; Bye, 1979). In addition to a relatively short life-cycle that enables transplant experiments (Williams and Hill, 1986), *B. rapa* is equipped with a well-annotated genome (Wang et al., 2011) and is closely related to the model organism *Arabidopsis thaliana* (Yang et al., 2005, Mun et al., 2010). Field mustard is native to Eurasia, where it was originally domesticated and selected for morphologically diverse crop forms (e.g., turnips, pak choi, napa cabbage, and oilseed crops), making it a model for extreme phenotypic divergence due to domestication (McAlvay, Chapter 2; Gómez-Campo and Prakash, 1999; Zhao et al., 2005; Guo et al., 2014). Weedy forms of field mustard have spread to temperate areas worldwide (McAlvay, Chapter 3; Hall, 2005). Weedy *B.*

rapa may have reached the Americas as early as the 16th century (McAlvay Chapter 2; McAlvay, Chapter 3; Gade, 1972; Bye, 1979) and now inhabits disturbed areas of coastal and highland regions from Canada to Argentina (GBIF.org). Genetic evidence suggests that these populations are feral escapes derived from European or North African domesticates (McAlvay, Chapter 3), potentially pre-adapting them to anthropogenic environments and/or human preferences. Since its introduction, weedy *B. rapa* has been adopted as food, medicine, and fodder by cultures ranging from northwestern Mexico to Patagonia (Gade, 1972; Berlin et al., 1974; Bye, 1979; Ladio, 2001; Vieyra-Odilon and Vibrans, 2001; McAlvay, Chapter 4). Several cultures sow seeds in fertilized plots (Solís and Estrada, 2014; Blancas et al., 2013; Bye, 1979), and/or intentionally spare plants when weeding fields (Weismantel, 1989; Gade, 1972; Vieyra-Odilon and Vibrans, 2001). These activities can have evolutionary consequences for the targeted plant populations (Casas et al., 2007; Parra; 2010; Blanckaert et al. 2013).

The Rarámuri people of northwestern Mexico manage field mustard in an especially intensive manner that may have consequences for diversity and selection in local *B. rapa* populations (McAlvay, Chapter 4; Bye, 1979). The Rarámuri are a Uto-Aztecan speaking group inhabiting the northern Sierra Madre Occidental mountains of Chihuahua. Rarámuri people living in homesteads throughout the mountains pursue traditional maize-bean-squash agriculture and diverse cash-economy livelihood practices (Wyndham 2009). Many Rarámuri farming families take advantage of potherbs, or *quelites*, growing spontaneously in crop fields and margins (Bye, 1981; Bye, 1979; LaRochelle and Berkes, 2003). Among these *quelites*, spontaneous *B. rapa* (known as *mekuásari* in the Rarámuri language) is prominent in the diet as a boiled leafy green (Bye 1973, Bye 1981; LaRochelle and Berkes, 2003). Self-sown field mustard emerges spontaneously in the summer and quickly enters its reproductive stage, diverting biomass to stems and flowers and becoming fibrous and bitter, making it less desirable as a food resource (Bye 1979). To extend the vegetative stage of field mustard, Rarámuri people sow seeds in tilled plots during early fall so that emerging plants will not be triggered to flower by the long day length of summer (Bye, 1979; McAlvay, Chapter 4). These plants are typically sown in plots where livestock corrals have been stationed and droppings have been deposited (Bye 1979; LaRochelle and Berkes, 2003). Rarámuri cultivation of *B. rapa* is recorded as early as 1776 (Bye, 1979, 1776). Humans can induce rapid evolutionary changes in plants and animals even on decadal time scales (Palumbi, 2001; Bone and Farres, 2001), so Rarámuri cultivation may be influencing the evolution of these field mustard populations.

Phenological and morphological traits may be under selection by Rarámuri farmers. Life-history characteristics play an important role in many domestication processes (de Wet and Harlan, 1975). Rarámuri management and preference for an extended vegetative stage in field mustard may be selecting for delayed flowering time. Franks and Weis (2009) demonstrated that flowering time in *B. rapa* is capable of rapid adaptation, suggesting that this trait may also be capable of rapid shifts under artificial selection. Numerous Rarámuri farmers expressed preference for larger plants and intentionally gathered seed from those plants (McAlvay, Chapter 4). The preferences of plant managers have been demonstrated to drive selection in other studies of ongoing domestication (Johns and Keen 1986, Elias et al., 2007, Blanckaert et al. 2013). These changes are in line with the domestication syndromes (sensu de Wet and Harlan, 1975) observed in similar crops.

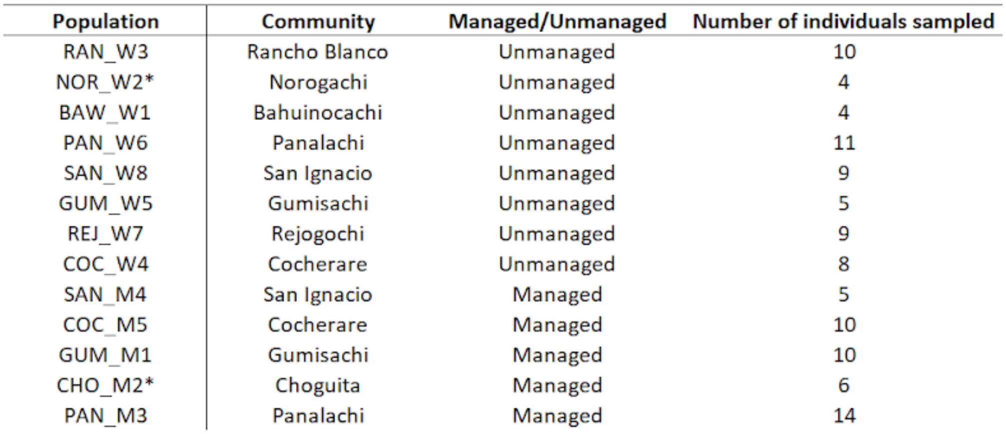
Past studies of ongoing domestication-like processes in Mexico have shown a variety of population genetic trends when comparing managed and unmanaged populations. While a bottleneck in diversity is predicted under domestication due to small founder populations (Doebley, 1992; Tanksley and McCouch, 1997), some studies of ongoing domestication have found higher genetic diversity in managed populations due to introgression from wild populations, and humans transporting propagules from other areas (Tinoco et al., 2005; Zárate et al., 2005). In other parts of Mexico gene flow between managed crops and local conspecifics or congeners is seen as a beneficial source of novel diversity (Wilkes, 1977; Nabhan, 1984). Pollinating insects are known to visit *B. rapa*, especially bees and flies (Rader et al., 2013, 2009; Warwick et al., 2003), and unplanted *B. rapa* in field margins may cross with *B. rapa* sown in fertilized plots, but as the bulk of unmanaged field mustard emerge with the first rains in the summer, a temporal reproductive isolation may exist (Bye, 1979). While Rarámuri farmers often sow seeds saved from previously planted parcels of field mustard, they occasionally collect seeds from spontaneously occurring individuals potentially further preventing a signal of reduced diversity (McAlvay, Chapter 4). Increased genetic differentiation from local wild populations is also predicted due to prolonged isolation and selection (Parra et al., 2008), but the genetic structuring of managed populations may also be influenced by seed exchange networks (Fuentes et al., 2012; Jensen et al., 2013) and gene flow with sympatric unmanaged populations (Sukopp et al., 2005). Many Rarámuri regularly engage in informal exchange of seeds when visiting each other’s houses and share seeds with those in need, exercising the principle of *korima* (Ezequiel and Guadalupe, 2014). In many studies of ongoing domestication levels of gene flow are high between managed and wild populations (Casas et al., 2007).

This study analyzed the genetic and phenotypic differences between unmanaged and Rarámuri-managed populations of field mustard. Specifically, we compared managed and unmanaged populations using single nucleotide polymorphisms (SNPs) derived from genotyping-by-sequencing (GBS) (Elshire et al., 2011) to assess genetic diversity and differentiation, and a common garden experiment to investigate phenology and morphology. We hypothesized that managed populations would have similar levels of diversity to unmanaged populations due to introgression from local wild populations and exchange of seed between farmers. We also expected genetical differentiation between nearby unmanaged populations. We predicted that managed populations would also have more rapid germination, a longer vegetative stage, and greater height.

Materials and Methods

Population sampling— This study was conducted in the Rarámuri communities of Bahuinocachi, Rancho Blanco, Norogachi, Gumisachi, Choguita, Cocherare, Panalachi, Rejogochi, and San Ignacio, all in Chihuahua, Mexico. Unmanaged populations were identified through application of three criteria: (1) no local knowledge of past management, (2) greater than 3 km from dwellings and managed plots, and (3) no evidence of management (tilling or weeding). Managed populations were identified as those sown in manured plots from seed collected from previously sown *B. rapa*. For population genetic sampling, we collected young leaf material from an average of eight samples each from eight unmanaged and five managed populations (Fig. 1A, see numbers per population in Table 1.), and dried and stored it in silica gel. For the common garden experiment, seed was collected from seven wild and four managed populations (Fig. 1B, Table 1.) because mature siliques were not available for two populations. Plants were sampled by walking a straight line across the patch and collecting the nearest plant at 1-meter intervals. We obtained seed and leaf samples through fieldwork conducted over three trips (a total of six weeks), with plants sampled under Robert Bye's permit for the project "*Conservación de la agrobiodiversidad de la Milpa Tarahumara, Chihuahua.*" Herbarium specimens were collected for each population and deposited at the Wisconsin State Herbarium (WIS) and National Autonomous University of Mexico herbarium (MEXU).

Table 1. Populations of *B. rapa* sampled in Rarámuri communities in Chihuahua, Mexico. The number of samples per population takes into account the one individual removed from CHO_M2 and one individual removed from REJ_W7 due to low coverage (see SNP and taxon filtering section). * indicates populations sampled for population genetic analyses but not for the common garden experiment.



Population	Community	Managed/Unmanaged	Number of individuals sampled
RAN_W3	Rancho Blanco	Unmanaged	10
NOR_W2*	Norogachi	Unmanaged	4
BAW_W1	Bahuinocachi	Unmanaged	4
PAN_W6	Panalachi	Unmanaged	11
SAN_W8	San Ignacio	Unmanaged	9
GUM_W5	Gumisachi	Unmanaged	5
REJ_W7	Rejogochi	Unmanaged	9
COC_W4	Cocherare	Unmanaged	8
SAN_M4	San Ignacio	Managed	5
COC_M5	Cocherare	Managed	10
GUM_M1	Gumisachi	Managed	10
CHO_M2*	Choguita	Managed	6
PAN_M3	Panalachi	Managed	14

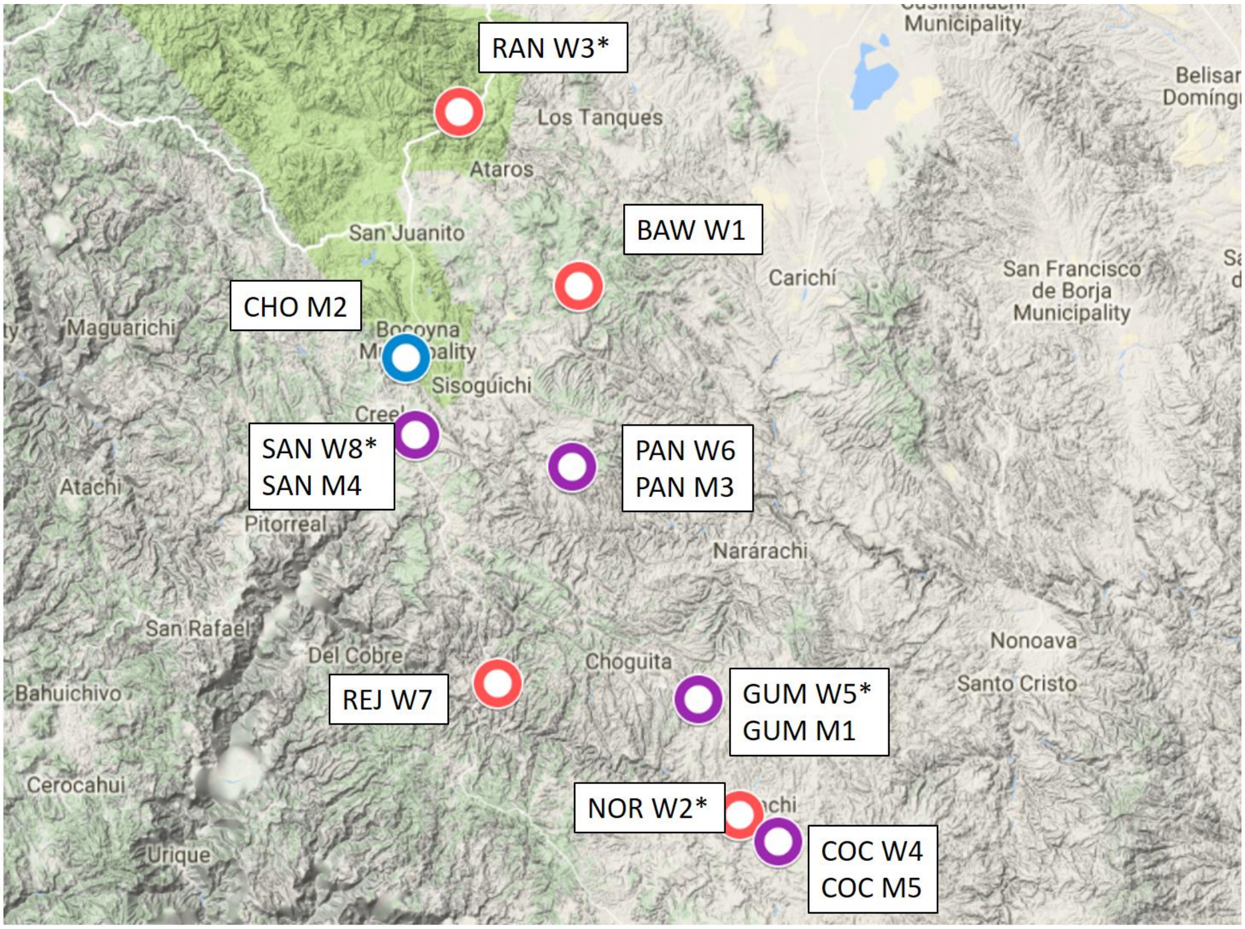


Fig 1. Locations of Rarámuri communities where field mustard populations were sampled for genetic analyses and the common garden experiment. Blue rings indicate communities where only managed populations were collected, red rings show communities where only unmanaged populations were collected, and purple rings indicate communities where a managed and unmanaged population were collected. Asterisks indicate populations that were sampled for genetic analyses but not the common garden experiment. Map data: 2018 Google, INEGI.

Population genetic analyses

***DNA extraction and sequencing*—**Genotyping-by-sequencing and SNP calling was conducted as in McAlvay (Chapter 2). Briefly, DNA was extracted using CTAB (Doyle and Doyle 1987), libraries constructed using the restriction enzyme ApeKI, and fragments sequenced using an Illumina HiSeq 2000 (Illumina Inc. San Diego, CA, United States) at the University of Wisconsin

Biotech Center (UWBC). We used the GBS 2 pipeline in Tassel 5 (Glaubitz et al., 2014) to process reads and call single nucleotide polymorphisms (SNPs) and Burrows-Wheeler Alignment (Li and Durbin, 2009) to align reads to a reference genome (Wang et al., 2011).

SNP and sample filtering—We filtered SNPs using VCFtools (Danecek et al., 2011) based on read depth (minimum mean depth = 3), number of alleles (only biallelic loci used), minimum percent of genotypes scored per site (90%; 100% used for PCA), and minimum minor allele frequency (1%). We further used Tassel 5 (Glaubitz et al., 2014) to remove sites with greater than 50% heterozygosity. Taxa were removed that had <50% of the loci scored. After filtering, 33,360 SNPs were retained.

Genetic diversity and structure— We used Tassel 5 (Glaubitz et al., 2014) to characterize nucleotide diversity (Nei and Li, 1979) and used ANOVA to compare differences in nucleotide diversity across groups of populations (managed and unmanaged) with an alpha of 0.05. To assess the genetic structure of managed and unmanaged populations of *B. rapa*, we used fastSTRUCTURE 1.0 (Raj et al. 2014). We tested different group numbers (K) between 1 and 15 with ten replicates at each value. To determine which K value maximized marginal likelihood, we used the ChooseK.py utility included in the fastSTRUCTURE package. fastSTRUCTURE plots were visualized through STRUCTURE PLOT 2.0 (Ramasamy et al., 2014). To further investigate genetic structure, we used Principal Component Analysis (PCA) in Plink (Purcell et al., 2007) and visualized the resulting ordination using Genesis (Buchmann and Hazelhurst, 2014). We also evaluated fixation indices (F_{ST}) (Weir and Cockerham, 1984) to investigate genetic differentiation between each pair of populations using Arlequin 3.5 (Excoffier et al., 2005). To assess patterns of population structure across groups of populations (managed and unmanaged) we implemented Analysis of Molecular Variance (AMOVA) (Excoffier et al., 1992) in Arlequin 3.5 (Excoffier et al., 2000). To determine the relationships between populations included in the study, we generated a coalescent tree using SVDquartets (Chifman and Kubatko, 2014) implemented in Paup (Swofford, 2003). SVDquartets is a coalescent-based approach which evaluates quartets of taxa and combines them to infer the most likely tree. We evaluated all possible quartets and produced 100 bootstrap replicates.

Phenotypic analyses

Common garden— To assess phenotypic differences across populations, we conducted a common garden experiment. To minimize maternal effects due to differing environmental conditions of each populations, in the winter of 2016/17 we grew seeds bulked from all maternal plants in each population at the Walnut Street Greenhouses (WSG) at University of Wisconsin–Madison in 6” square plastic pots with Promix HP soil (Premier Tech, Rivière-du-Loup, Québec). Supplemental light was provided for 16 hours per day. Pollination bags were used to keep individuals from each population reproductively isolated. Seeds harvested from this initial round of reproduction were used for the common garden experiment. In September 2017, we set up a common garden experiment with the same location, medium, pots, and conditions, but with a randomized block design. We used six blocks, each containing nine flats, which in turn each contained thirteen pots. Into each of the thirteen pots of each flat, we randomly allocated a seed descended from one of the thirteen populations sampled, providing a total of 54 individual plants from each population across the entire experiment.

Phenotypic measurements and analyses—To compare the phenology and morphology of managed and unmanaged populations, we measured two phenotypic characters: height from ground to first open flower (cm) and days to flowering. Height and flowering time were selected as farmers mentioned preference for taller plants with delayed flowering. Measurements of phenology and morphology were analyzed using ANOVA to assess pairwise differences between populations in the same communities and between all managed and unmanaged populations. To visualize similarity of sampled individuals based on phenotypic characters, we employed PCA and constructed a Neighbor-Joining tree (Saitou and Nei, 1987) based on morphological distances of populations.

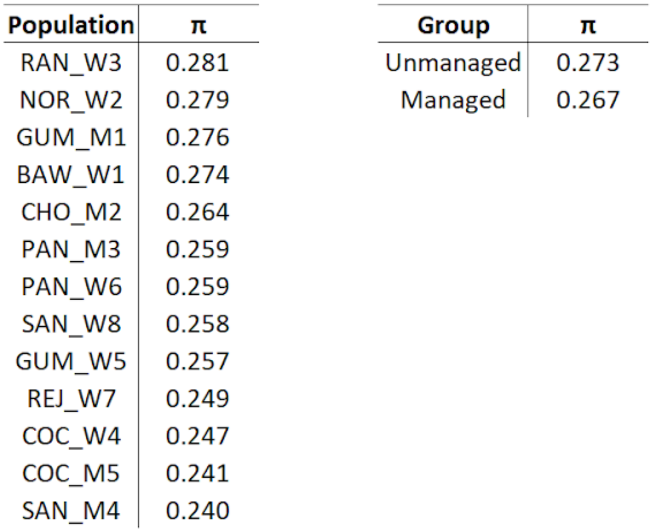
Results

Population genetic analyses

***GBS sequencing and filtering*—**See Chapter 2 for raw reads and SNP-calling results. After filtering, 333,55 SNPs and 103 taxa remained. One sample from CHO_M2 and one sample from REJ_W7 were removed due to low coverage (<50% of the loci scored).

***Genetic diversity and structure*—**Nucleotide diversity (Table 2.) did not follow a consistent pattern of higher diversity in managed or lower diversity in unmanaged populations. In pairwise comparisons between managed and unmanaged populations in the same communities, indicated that GUM_M1, PAN_M3, SAN_W3, and COC_W4 had higher diversity than their counterparts. ANOVA demonstrated that differences in nucleotide diversity among managed and unmanaged populations as a whole were not significant (*p* = 0.39)

Table 2: Nucleotide diversity of individual populations of field mustard in Chihuahua and total nucleotide diversity of all managed versus all unmanaged populations.



Population	π
RAN_W3	0.281
NOR_W2	0.279
GUM_M1	0.276
BAW_W1	0.274
CHO_M2	0.264
PAN_M3	0.259
PAN_W6	0.259
SAN_W8	0.258
GUM_W5	0.257
REJ_W7	0.249
COC_W4	0.247
COC_M5	0.241
SAN_M4	0.240

Group	π
Unmanaged	0.273
Managed	0.267

The fastSTRUCTURE ChooseK function suggested that K=1 maximized marginal likelihood and a K=3 best explained the structure of the data. Figure 2 depicts the allocation of individuals to clusters for K values between 2 and 4. At K=2, wild populations from Bahuinocachi (BAW_W1), Norogachi (NOR_W2), and Rancho Blanco (RAN_W3) and the managed population from Gumisachi (GUM_M1) clustered together, while all other samples formed another group. At K=3, the pattern was consistent with K=2 but managed populations from Cocherare (COC_M5) separated into their own group with no admixture present. At K=4, the managed San Ignacio population (SAN_M4) separated into its own group. By K=4, three out of four of the managed populations clustered in their own groups or with wild samples from other communities. At all levels of K, admixture was evident among most populations.

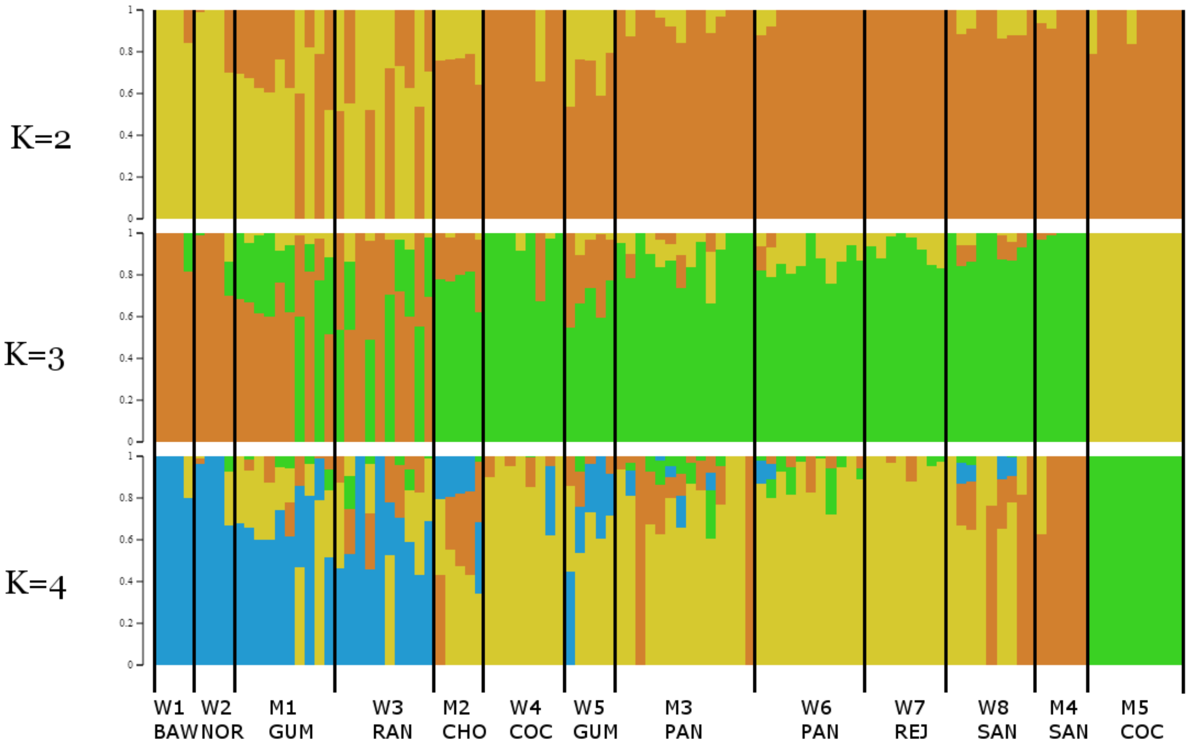


Figure 2. fastSTRUCTURE plot of populations of *B. rapa* from Chihuahua for values of K between 2-4. Each individual sample is represented by a single column, and each population delineated by vertical black lines.

PCA showed patterns like those observed with fastSTRUCTURE. PC1 separated unmanaged samples from Norogachi (NOR_W2), Bahuinocachi (BAW_W1), and Rancho Blanco (RAN_W3) and Cocherare (GUM_M1) from other samples (Fig. 3). PC2 separated managed samples from San Ignacio (SAN_M4) and managed samples from Cocherare (COC_M5) into their own clusters, the latter not overlapping other clusters. Some wild samples from San Ignacio (SAN_W8) were associated with San Ignacio managed samples (SAN_M4)

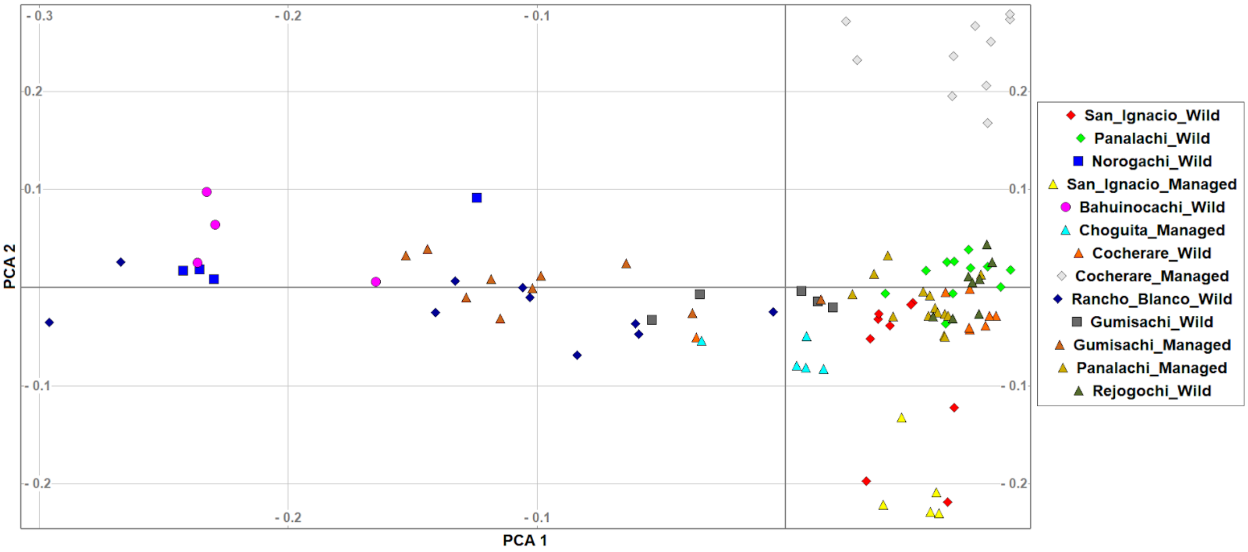
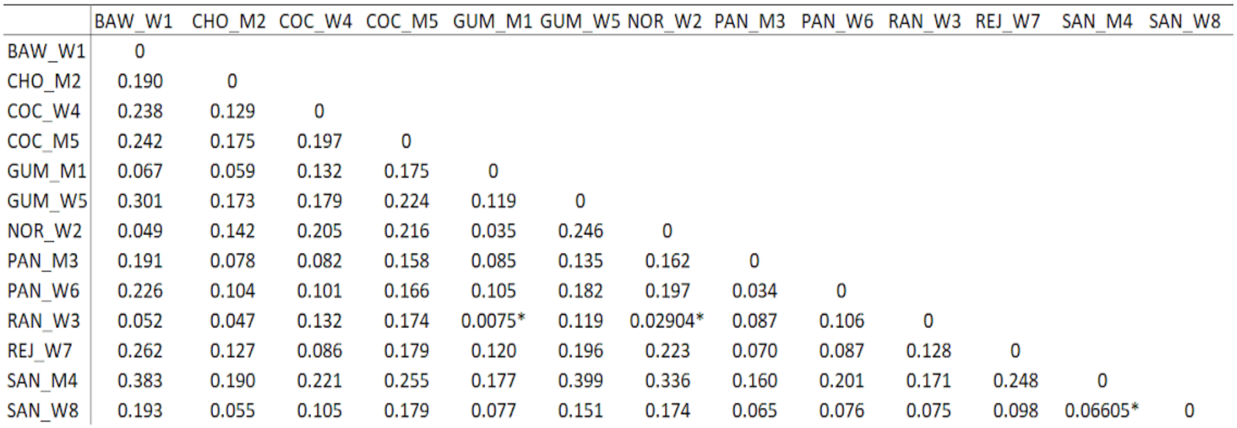


Figure 3. PCA of SNP data for samples of *B. rapa* populations collected in Chihuahua, Mexico. PC1 explains 11.27% of the variance and PC2 explains 7.31% of the variance.

F_{ST} values ranged from 0.034 between managed and unmanaged populations in Panalachi (PAN_M3 and PAN_W6) to 0.399 between the managed San Ignacio population (SAN_M4) and the unmanaged Gumisachi population (GUM_W5). Significant levels of differentiation were detected between all but one (San Ignacio) pair of managed and unmanaged populations from the same communities, though levels of differentiation between the pairs was less than differentiation between the wild populations in the pairs and next closest wild populations.

Table 3. Pairwise F_{ST} values of populations of managed and unmanaged *B. rapa* in Chihuahua, Mexico. Asterisks indicate insignificant P-value (alpha of 0.05).



	BAW_W1	CHO_M2	COC_W4	COC_M5	GUM_M1	GUM_W5	NOR_W2	PAN_M3	PAN_W6	RAN_W3	REJ_W7	SAN_M4	SAN_W8
BAW_W1	0												
CHO_M2	0.190	0											
COC_W4	0.238	0.129	0										
COC_M5	0.242	0.175	0.197	0									
GUM_M1	0.067	0.059	0.132	0.175	0								
GUM_W5	0.301	0.173	0.179	0.224	0.119	0							
NOR_W2	0.049	0.142	0.205	0.216	0.035	0.246	0						
PAN_M3	0.191	0.078	0.082	0.158	0.085	0.135	0.162	0					
PAN_W6	0.226	0.104	0.101	0.166	0.105	0.182	0.197	0.034	0				
RAN_W3	0.052	0.047	0.132	0.174	0.0075*	0.119	0.02904*	0.087	0.106	0			
REJ_W7	0.262	0.127	0.086	0.179	0.120	0.196	0.223	0.070	0.087	0.128	0		
SAN_M4	0.383	0.190	0.221	0.255	0.177	0.399	0.336	0.160	0.201	0.171	0.248	0	
SAN_W8	0.193	0.055	0.105	0.179	0.077	0.151	0.174	0.065	0.076	0.075	0.098	0.06605*	0

The SVDquartets analysis (Fig. 4) was largely consistent with the PCA and fastSTRUCTURE analysis and clustered unmanaged populations from Bahuinocachi (BAW_W1), Norogachi (NOR_W2), and Rancho Blanco (RAN_W3) and the managed population from Gumisachi (GUM_M1) together. Pairs of managed and unmanaged populations from Panalchi (PAN_W6 and PAN_M3) and San Ignacio (SAN_M4 and SAN_W8) clustered together whereas other pairs of managed and unmanaged populations (i.e. those from Cocherare and Gumisachi) were not most closely related to each other.

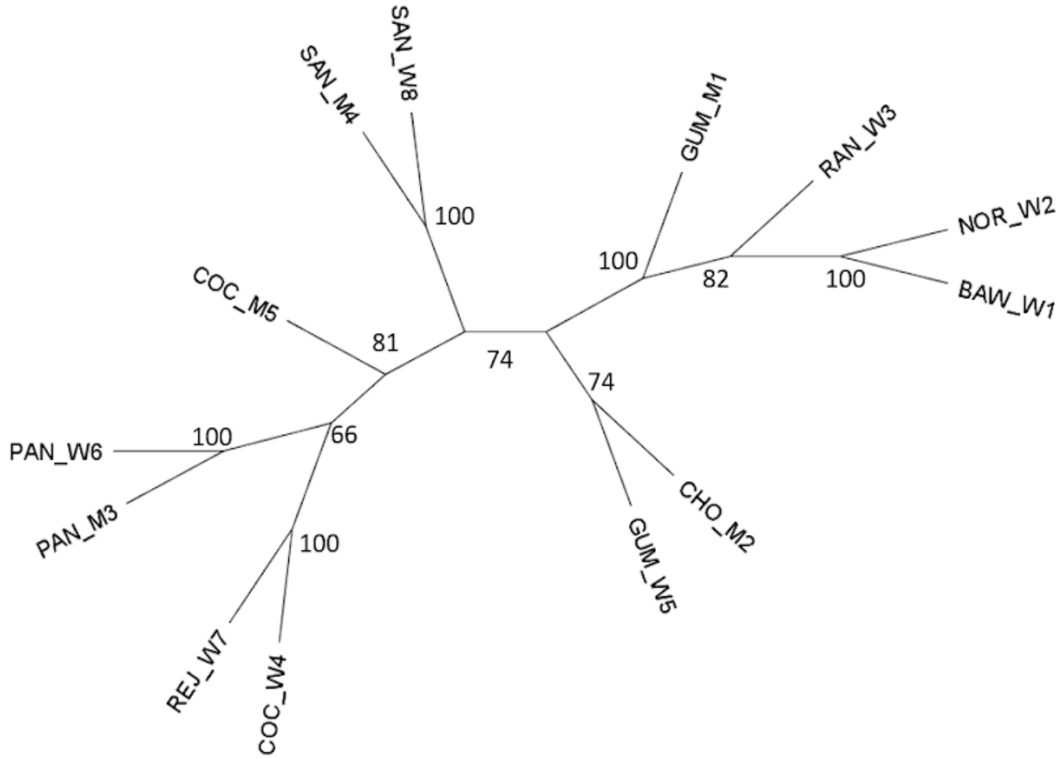


Figure 4. Cladogram of relationships between populations of *B. rapa* collected in Chihuahua Mexico recovered by SVDquartets.

Phenotypic analyses

The mean days from germination to flowering of all populations was 26.61 (s = 5.33). Managed populations (mean = 27.93) had an average of roughly two and a half more days to flowering compared to unmanaged populations (mean = 25.36) at $\alpha = 0.05$ ($p < 0.0001$). Days until flowering (Fig. 6) in pairwise comparisons of populations within the same community were significant between PAN_M3 (mean 31. 74) and PAN_W6 (mean 24.76) ($p < .0001$) at $\alpha = 0.05$ but not between COC_W4 and COC_M5 ($p = 0.16$).

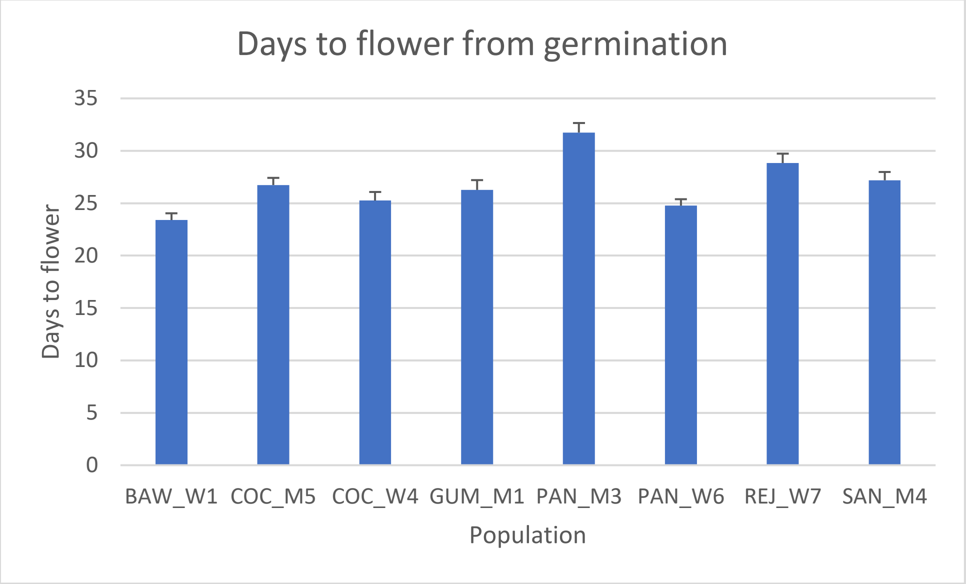


Figure 6. Average days from germination of seeds to flowering from populations of *B. rapa* in Chihuahua. Standard errors are presented.

The mean height of all populations was 29.51cm (s = 10.60). The height of managed and unmanaged populations was not significantly different at α = 0.05 (p = 0.79). Height (Fig. 5) in pairwise comparisons of populations within the same community were not significant between PAN_M3 and PAN_W6 (p = .052) or COC_W4 and COC_M5 (p = 0.15).

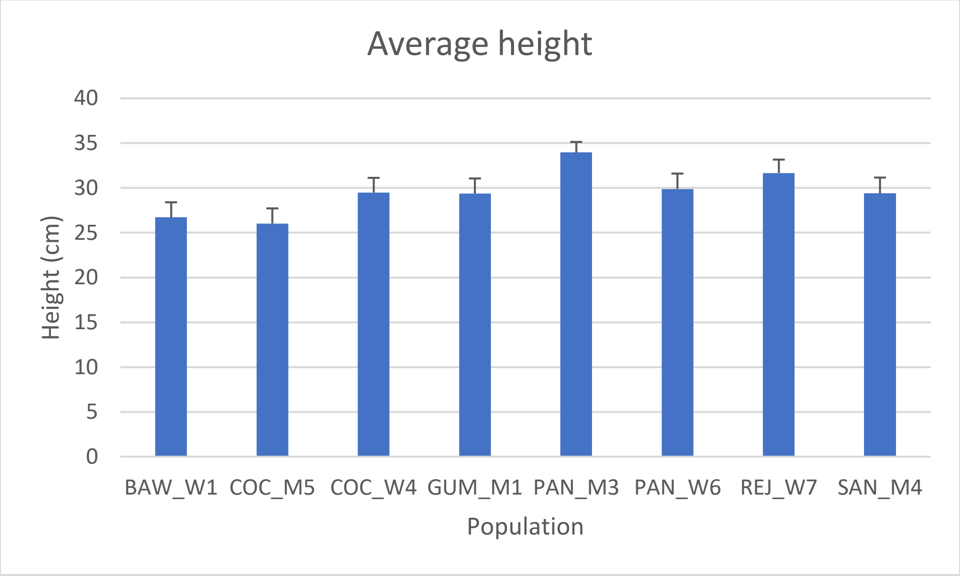


Figure 7. Average height of plants in centimeters from populations of *B. rapa* in Chihuahua. Standard errors are presented.

Discussion

***Genetic diversity and structure*—**Several populations consistently clustered together in our fastSTRUCTURE, SVDquartets, and PCA results. For example, the managed population from Gumisachi consistently groups with RAN_W3, NOR_2, BAW_W1. The managed population from Gumisachi also had high diversity compared to the local unmanaged population. These findings are consistent with our interviews (Chapter 4) with the farmer managing this population, who had a personal seed bank and frequently exchanged *B. rapa* seed with farmers in different communities. We also found that managed populations from San Ignacio and Cocherare were differentiated from all other groups in fastSTRUCTURE and PCA and had the lowest levels of nucleotide diversity of any populations, suggesting potential effects of anthropogenic isolation or selection. Across all managed and unmanaged populations, there was not a clear trend in nucleotide diversity consistent with the findings of Otero-Arnaiz et al. (2005) and Parra et al. (2008, 2010) with traditionally managed cacti. While reductions in diversity are often associated with domestication (Doebley, 1992), management of otherwise wild plants may involve relatively low levels of selection and/or human assisted migration of germplasm from other areas (Parra et al, 2008).

***Phenotypic differences*—**We observed differences in flowering time between managed and unmanaged populations. Flowering time in managed populations occurred later than in unmanaged populations, and in the case of the populations from Panalachi, the descendents of the managed population flowered an average of 7 days later than unmanaged counterparts. The transition from vegetative to reproductive life stages in plants can be an important trait for domestication and artificial selection (Cockram et al., 2007). Height was not significantly different between populations or across management conditions. Since height was measured as height to first open flower, and Rarámuri interviewees generally expressed preferences for characteristics in the vegetative life stages, this measurement may have not captured farmer induced selection.

Our findings suggest that phenological shifts can be detectable even with relatively limited isolation and reductions in diversity in populations under human management. Since the leaf and stem material of *B. rapa* in its reproductive stage is fibrous and unpalatable to most Rarámuri farmers (Bye, 1979; McAlvay, Chapter 4), and field mustard is capable of rapid bolting (Williams and Hill, 1984), it is not surprising to find evidence for relatively dramatic selection on this trait.

While ongoing management of local plants, should not be teleologically considered a stage in progression to more intensive selection or domestication (Turner et al., 2011) and any ethnographic analogy should be cautiously applied (Currie, 2016), these findings also provide insight into the domestication of crops plants that are thought to have originally existed as weeds in farmers' fields, including rice, sorghum, carrots (Harlan 1992), tomatoes (Gade, 1972), rye, oats (Vavilov 1926), and lena camelina (Zohary and Hopf, 1994). In the early stages of domestication of carrots, tomatoes, and other weed-derived crops, substantial levels of gene-flow with sympatric unmanaged forms could have been prevalent, potentially weakening the strength of selection for desirable traits. While farmers may have mitigated undesirable gene-flow by growing propagules in isolated plots, the Rarámuri management of field mustard demonstrates that this may have also been accomplished by temporal isolation based on sowing time and phenology.

***Conservation of anthropogenic germplasm*—**In many parts of highland Latin America *B. rapa* has become an important mainstay in local diets, especially in typically food-insecure seasons (Bye, 1979; Vieyra-Odilon and Vibrans, 2001; McAlvay, Chapter 4). If humans have exerted selection on populations of field mustard, they represent a form of cultural heritage that is not currently protected by conservation efforts focused on crops or wild plants. In the case of *B. rapa,* its status as an invasive plant could lead to conflicts between those seeking to remove it for ecological or agricultural reasons, and those who depend on it for food and encourage it (McAlvay, Chapter 4).

Future directions—In domestication research there are standing controversies over the rate (Fuller et al., 2014), intentionality, and evolution involved (Larson et al., 2014) that studies of ongoing domestication-like processes could potentially address. Despite the availability of numerous techniques to explore ongoing selection (Merila and Hendry, 2014), only a handful have been applied to ongoing domestication processes. The basic understanding of genetic diversity and structure provided by this study lays the groundwork for future research using this inferentially powerful study system to test hypotheses about evolution under domestication. The genomic resources and short life-cycle of *B. rapa* enable the use of inferentially powerful techniques and the ongoing nature of management in the area could allow longitudinal studies that address the strength of selection and rate of evolution.

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Supplementary material

Supplementary material 1. Samples included in chapter 2 after sample filtering.

Sample name/accession number	**Subspecies and location information**	**Geographic region**	**Crop type**
PI250004	*B. rapa* Egypt	Africa	Turnip
BRA1718TLibya	*B. rapa* ssp. *rapa*	Africa	Turnip
CR2552OLibya	*B. rapa* ssp. *rapa*	Africa	Turnip
BRA2218Canada	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous
Quebecemilyharvest	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous
Quebecsimard2	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous
Simard3WCanada	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous
TN2974QuebecMilby	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous
BRA2809Turk	*B. rapa* ssp. *sylvestris*	Caucasus	Spontaneous
Cr2211geor	*B. rapa* ssp. *sylvestris*	Caucasus	Spontaneous
CR2234Russiasilv	*B. rapa* ssp. *sylvestris*	Caucasus	Spontaneous
CR2241georg	*B. rapa* ssp. *sylvestris*	Caucasus	Spontaneous
CR2269senzatesta	*B. rapa* ssp. *sylvestris*	Caucasus	Spontaneous
CR2354georg	*B. rapa* ssp. *sylvestris*	Caucasus	Spontaneous
Georgiahoney	*B. rapa* ssp. *sylvestris*	Caucasus	Spontaneous
G30479	*B. rapa* ssp. *rapa*	East Asia	Turnip
G31786	*B. rapa* China	East Asia	Pak Choi
G31787	*B. rapa* China	East Asia	Pak Choi
PI257229	*B. rapa* China	East Asia	Napa Cabbage
PI257241	*B. rapa* China	East Asia	Pak Choi
PI662729	*B. rapa* China	East Asia	Pak Choi
PI662759	*B. rapa* China	East Asia	Pak Choi
PI662760	*B. rapa* China	East Asia	Pak Choi
PI662761	*B. rapa* China	East Asia	Pak Choi
PI662762	*B. rapa* China	East Asia	Pak Choi
PI391547	*B. rapa* China, Shaanxi	East Asia	Napa Cabbage
PI391549	*B. rapa* China, Shaanxi	East Asia	Napa Cabbage
CR2212Chinaolei	*B. rapa* ssp. *oleifera*	East Asia	Oilseed
PI269442TPak	*B. rapa* ssp. *rapa* Pakistan	East Asia	Turnip
G28899	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
G28900	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
G28902	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
G29043	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage

G29917	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
G30708	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
G30955	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
G30956	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
G31776	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
G31777	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
G31784	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
G31785	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
G32371	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
PI257239	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
PI430484	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
PI430485	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI430486	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
PI478324	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
PI633165	*B. rapa* subsp. *chinensis* China	East Asia	Pak Choi
PI662540	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662542	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662543	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662544	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662545	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662546	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662547	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662548	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662549	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage
PI662550	*B. rapa* subsp. *chinensis* China	East Asia	Napa Cabbage

PI662553	*B. rapa* subsp. *chinensis*	China	East Asia	Napa Cabbage
PI662554	*B. rapa* subsp. *chinensis*	China	East Asia	Napa Cabbage
PI662555	*B. rapa* subsp. *chinensis*	China	East Asia	Napa Cabbage
PI662556	*B. rapa* subsp. *chinensis*	China	East Asia	Turnip
PI662557	*B. rapa* subsp. *chinensis*	China	East Asia	Napa Cabbage
PI662558	*B. rapa* subsp. *chinensis*	China	East Asia	Napa Cabbage
PI662658	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662723	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662724	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662725	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662726	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662727	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662738	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662739	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662751	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662752	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662753	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662754	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662755	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662756	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662757	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
PI662758	*B. rapa* subsp. *chinensis*	China	East Asia	Pak Choi
G30792	*B. rapa* subsp. *chinensis*	Japan	East Asia	Pak Choi
G30794	*B. rapa* subsp. *chinensis*	Japan	East Asia	Pak Choi
PI662677	*B. rapa* subsp. *chinensis*	Japan	East Asia	Pak Choi

PI662678	*B. rapa* subsp. *chinensis* Japan	East Asia	Pak Choi
PI662680	*B. rapa* subsp. *chinensis* Japan	East Asia	Pak Choi
PI662681	*B. rapa* subsp. *chinensis* Japan	East Asia	Pak Choi
PI508408	*B. rapa* subsp. *chinensis* South Korea	East Asia	Pak Choi
PI508409	*B. rapa* subsp. *chinensis* South Korea	East Asia	Pak Choi
PI662682	*B. rapa* subsp. *chinensis* Taiwan	East Asia	Napa Cabbage
PI662690	*B. rapa* subsp. *narinosa* Japan	East Asia	Pak Choi
PI662691	*B. rapa* subsp. *narinosa* Japan	East Asia	Pak Choi
PI662626	*B. rapa* subsp. *nipposinica* Japan	East Asia	Turnip
PI662688	*B. rapa* subsp. *nipposinica* Japan	East Asia	Turnip
PI662689	*B. rapa* subsp. *nipposinica* Japan	East Asia	Turnip
PI662687	*B. rapa* subsp. *nipposinica* Taiwan	East Asia	Turnip
G30238	*B. rapa* subsp. *oleifera* Spain	East Asia	Pak Choi
PI390963	*B. rapa* subsp. *parachinensis* Hong Kong	East Asia	Pak Choi
PI390964	*B. rapa* subsp. *parachinensis* Hong Kong	East Asia	Pak Choi
G31344	*B. rapa* subsp. *parachinensis*, China	East Asia	Pak Choi
PI662783	*B. rapa* subsp. *parachinensis*, Indonesia, Sumatra	East Asia	Pak Choi
PI662722	*B. rapa* subsp. *pekinenis* China	East Asia	Napa Cabbage
PI234600	*B. rapa* subsp. *pekinensis* Australia	East Asia	Napa Cabbage
G30688	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
G30692	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
G30694	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
G30695	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
G30703	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
G31759	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
G31761	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage

G31765	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
G31773	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI269436	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI269437	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI418984	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI418985	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI418986	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI418987	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI418988	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI419007	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419024	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419025	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419026	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419027	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419028	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419038	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419105	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419106	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI419127	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419129	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419130	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI419131	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI432771	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI432774	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI432776	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage

PI432777	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI432779	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI436668	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI436669	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI436670	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI436671	*B. rapa* subsp. *pekinensis* China	East Asia	Pak Choi
PI478342	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI478345	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI478348	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI478349	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI487420	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI487421	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI487422	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI489751	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518839	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518840	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518841	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518842	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518843	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518844	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518845	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518846	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI518847	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI527322	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI527323	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage

PI662572	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662639	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662640	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662656	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662657	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662716	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662717	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662718	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662719	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662720	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662721	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662737	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662741	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662743	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662744	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662745	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662746	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662747	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662748	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662749	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662750	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI662791	*B. rapa* subsp. *pekinensis* China	East Asia	Napa Cabbage
PI419069	*B. rapa* subsp. *pekinensis* China, Beijing	East Asia	Napa Cabbage
PI419070	*B. rapa* subsp. *pekinensis* China, Beijing	East Asia	Napa Cabbage
PI419072	*B. rapa* subsp. *pekinensis* China, Beijing	East Asia	Napa Cabbage

PI419073	*B. rapa* subsp. *pekinensis*	China, Beijing	East Asia	Napa Cabbage
PI419074	*B. rapa* subsp. *pekinensis*	China, Beijing	East Asia	Napa Cabbage
PI430583	*B. rapa* subsp. *pekinensis*	China, Beijing	East Asia	Napa Cabbage
PI430610	*B. rapa* subsp. *pekinensis*	China, Beijing	East Asia	Napa Cabbage
PI590995	*B. rapa* subsp. *pekinensis*	China, Beijing	East Asia	Napa Cabbage
PI427091	*B. rapa* subsp. *pekinensis*	China, Guangdong	East Asia	Pak Choi
PI427094	*B. rapa* subsp. *pekinensis*	China, Jilin	East Asia	Napa Cabbage
PI391558	*B. rapa* subsp. *pekinensis*	China, Shaanxi	East Asia	Napa Cabbage
PI391559	*B. rapa* subsp. *pekinensis*	China, Shaanxi	East Asia	Napa Cabbage
PI391560	*B. rapa* subsp. *pekinensis*	China, Shaanxi	East Asia	Napa Cabbage
PI418957	*B. rapa* subsp. *pekinensis*	China, Shaanxi	East Asia	Napa Cabbage
PI418958	*B. rapa* subsp. *pekinensis*	China, Shaanxi	East Asia	Napa Cabbage
PI418959	*B. rapa* subsp. *pekinensis*	China, Shaanxi	East Asia	Napa Cabbage
PI279857	*B. rapa* subsp. *pekinensis*	Japan	East Asia	Napa Cabbage
PI662675	*B. rapa* subsp. *pekinensis*	Japan	East Asia	Napa Cabbage
PI662676	*B. rapa* subsp. *pekinensis*	Japan	East Asia	Napa Cabbage
PI662562	*B. rapa* subsp. *pekinensis*	Netherlands	East Asia	Napa Cabbage
PI269438	*B. rapa* subsp. *pekinensis*	Pakistan	East Asia	Pak Choi
PI508414	*B. rapa* subsp. *pekinensis*	South Korea	East Asia	Napa Cabbage
PI508416	*B. rapa* subsp. *pekinensis*	South Korea	East Asia	Napa Cabbage
PI508417	*B. rapa* subsp. *pekinensis*	South Korea	East Asia	Pak Choi
PI508418	*B. rapa* subsp. *pekinensis*	South Korea	East Asia	Napa Cabbage
PI508420	*B. rapa* subsp. *pekinensis*	South Korea	East Asia	Napa Cabbage
PI508421	*B. rapa* subsp. *pekinensis*	South Korea	East Asia	Napa Cabbage
PI508422	*B. rapa* subsp. *pekinensis*	South Korea	East Asia	Napa Cabbage

PI508423	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI508424	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI508425	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI508426	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI508427	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI508428	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI508429	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI508430	*B. rapa* subsp. *pekinensis* South Korea	East Asia	Napa Cabbage
PI257236	*B. rapa* subsp. *pekinensis* Thailand	East Asia	Napa Cabbage
PI257237	*B. rapa* subsp. *pekinensis* Thailand	East Asia	Pak Choi
PI257238	*B. rapa* subsp. *pekinensis* Thailand	East Asia	Napa Cabbage
G30441	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
G30784	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
G30787	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662611	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662612	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662617	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662619	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662620	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662613	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662614	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662615	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662618	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI662621	*B. rapa* subsp. *pekinensis* U.S.	East Asia	Napa Cabbage
PI644006	*B. rapa* subsp. *pekinensis* U.S. California	East Asia	Napa Cabbage

PI644007	*B. rapa* subsp. *pekinensis* U.S. California	East Asia	Napa Cabbage
PI662616	*B. rapa* subsp. perviridis U.S.	East Asia	Napa Cabbage
PI662627	*B. rapa* subsp. perviridis U.S.	East Asia	Turnip
PI662559	*B. rapa* subsp. *rapa* Japan	East Asia	Turnip
PI662693	*B. rapa* subsp. *rapa* Japan	East Asia	Turnip
PI662686	*B. rapa* subsp. *rapa* Taiwan	East Asia	Pak Choi
PI662629	*B. rapa* subsp. *rapa* U.S.	East Asia	Turnip
PI662630	*B. rapa* subsp. *rapa* U.S.	East Asia	Turnip
PI662631	*B. rapa* subsp. *rapa* U.S.	East Asia	Turnip
PI662632	*B. rapa* subsp. *rapa* U.S.	East Asia	Turnip
PI662695	*B. rapa* subsp. *rapa* U.S.	East Asia	Turnip
PI662628	*B. rapa* subsp. *rapa* U.S.	East Asia	Turnip
G31848	*B. rapa* Germany	Europe	Turnip
PI662772	*B. rapa* Germany	Europe	Turnip
PI662684	*B. rapa* Italy	Europe	Rapini
PI633161	*B. rapa* Italy, Calabria	Europe	Rapini
BR50226valenc	*B. rapa* ssp. *rapa*	Europe	Turnip
BRS0225Valenc	*B. rapa* ssp. *rapa*	Europe	Turnip
EXTBRS0228TCastellon	*B. rapa* ssp. *rapa*	Europe	Turnip
EXTBRSO231Caceres	*B. rapa* ssp. *rapa*	Europe	Turnip
EXTBRSO239Santander	*B. rapa* ssp. *rapa*	Europe	Turnip
PI633168	*B. rapa* subsp. *oleifera* Italy	Europe	Rapini
PI662794	*B. rapa* subsp. *oleifera* Italy	Europe	Rapini
PI662694	*B. rapa* subsp. *rapa* France	Europe	Turnip
G31841	*B. rapa* subsp. *rapa* Germany	Europe	Turnip
PI662685	*B. rapa* subsp. *rapa* Italy	Europe	Rapini
PI662795	*B. rapa* subsp. *rapa* Netherlands	Europe	Turnip
G30808	*B. rapa* subsp. *rapa* U.S.	Europe	Turnip
PI662692	*B. rapa* subsp. *rapa* U.S.	Europe	Turnip
PI662775	*B. rapa* subsp. *rapa* Unknown	Europe	Turnip
PI198061	*B. rapa* Sweden	Europe	Spontaneous
PI360878	*B. rapa* Sweden	Europe	Spontaneous
PI649162	*B. rapa* Sweden	Europe	Spontaneous
PI662683	*B. rapa* U.S.	Europe	Rapini
PI662773	*B. rapa* Unknown	Europe	Turnip
PI662774	*B. rapa* Unknown	Europe	Turnip
PI662780	*B. rapa* Unknown	Europe	Turnip
PI662781	*B. rapa* Unknown	Europe	Turnip
175608takirdag	*B. rapa* ssp. *rapa*	Europe	Turnip
BRA1018TAustria	*B. rapa* ssp. *rapa*	Europe	Turnip
BRA1709TTunisian	*B. rapa* ssp. *rapa*	Europe	Turnip
BRA1831TItaly	*B. rapa* ssp. *rapa*	Europe	Turnip
BRA1892TGeorgia	*B. rapa* ssp. *rapa*	Europe	Turnip

BRA1894TItaly	*B. rapa* ssp. *rapa*	Europe	Turnip
BRA2731TItaly	*B. rapa* ssp. *rapa*	Europe	Turnip
BRA917THungary	*B. rapa* ssp. *rapa*	Europe	Turnip
CR1542OPoland	*B. rapa* ssp. *rapa*	Europe	Turnip
PI169082samsun	*B. rapa* ssp. *rapa*	Europe	Turnip
PI633178TDenmark	*B. rapa* ssp. *rapa*	Europe	Turnip
PI649185OGermany	*B. rapa* ssp. *rapa*	Europe	Turnip
PI649189Belgium	*B. rapa* ssp. *rapa*	Europe	Turnip
questionFinlandBRA1814	*B. rapa* ssp. *rapa*	Europe	Turnip
questionYugoBRA2780	*B. rapa* ssp. *rapa*	Europe	Turnip
Rejogochib9	*B. rapa* ssp. *rapa*	Europe	Turnip
BRA2465sweden	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
CR1538OSlovakia	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
CR1578slovak	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
CR2210slovak	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
CR2213austria	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
CR2355Britain	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
Ewijk	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
GaliniMaarsen	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
Lindbjerg	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
Lonstorp	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
NGB1320661Horne	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
NGB1320671Branbjerg	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
NGB132068.1WOutrup	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
PI537003Serb	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
Wageningen	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous
BR50227cuenc	*B. rapa* ssp. *rapa*	Europe	Spanish turnip
M143grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M163grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M173grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M190grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M197grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M316grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M417grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M472grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M588grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos

M599grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
M82grelo	subsp. *sylvestris* var. esculenta	Europe	Grelos
bavicquar	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini
bavinccentoventesta	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini
bavincnoventina	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini
bavincricamrzno	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini
CR2551italian	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini
PI6331680Italy	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini
PI204683Kayseri	*B. rapa* ssp. *rapa* Turkey	Latin America	Spontaneous
14Alej46a	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
14Alej46c	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
14Alej47	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
14Alej62	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
14DFmark11b	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
14Pan59	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
14Pan61b	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
2Colpos1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
3Colpos2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
3Colpos3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
AboveChuneloatfield4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
AboveChuneloatfield5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
AboveChuneloatfield6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
AboveChuneloatfield7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Alejf1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Alejf2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous

Alejf3	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Alejf4	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Alejf5	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco3	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco4	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco5	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco6	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco7	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Analco8	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Ang8	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Berta1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Berta2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Bneigh1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Bneigh2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Bneighc	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Celiabawino1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Celiabawino2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Celiabawino3	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Celiabawino4	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Choguitaavena1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Choguitaworkshopb2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Choguitaworkshopb3	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Choguitaworkshopb4	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous

Choguitaworkshopb5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Choguitaworkshopb6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Claudia1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Claudia2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cocham10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cochararehouse1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cochararehouse2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cochararemilpa1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cochararemilpa2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cochararemilpa3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cochararemilpa4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Cocheram2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Creel3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Creel4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
espinaca10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
espinaca5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
espinaca6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
espinaca7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
espinaca8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
espinaca9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
EspinacaB1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
EspinacaB2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
EspinacaB3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
EspinacaB4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
InoatfieldRanchoblanco1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous

InoatfieldRanchoblanco2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
InoatfieldRanchoblanco3	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
InoatfieldRanchoblanco4	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
IntownSanJuanito1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Jim1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
lupeworkshop1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Margar1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Margar2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariomilpa1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariomilpa3	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariomilpa4	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariomilpa6	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariomilpa7	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Marioseedbankb10	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Marioseedbankb5	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Marioseedbankb6	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Marioseedbankb7	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Marioseedbankb8	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Marioseedbankb9	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariosembrado1	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariosembrado2	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariosembrado3	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Mariosembrado4	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Nacho20071	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous
Nacho20072	*B. rapa* ssp. *sylvestris*	Mexico	Latin America	Spontaneous

Nacho20073	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Nacho20074	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Nacho2007b5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Nacho2007b6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Nacho2007b7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Nacho2007b8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Ozumbacriollo1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Ranchoblanco13	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Ranchoblanco2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Ranchoblanco5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Ranchoblanco6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Ranchoblanco7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Ranchoblanco9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu11	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu12	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu25	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refu9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous

Refugio2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Refugio3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejo1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejo2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejo3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejo4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejogochib10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejogochib5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejogochib6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejogochib7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Rejogochib8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Sanignacmb10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Sanignacmb6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Sanignacmb7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Sanignacmb8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Sanignacmb9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Santiag1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Santiag2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Santiag3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Sisoguichi1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Vainooo1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Vainooo2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
Vainooo3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous
PI633181	*B. rapa* subsp. *rapa* Honduras, Lempira	Latin America	Spontaneous
311711Chile	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous

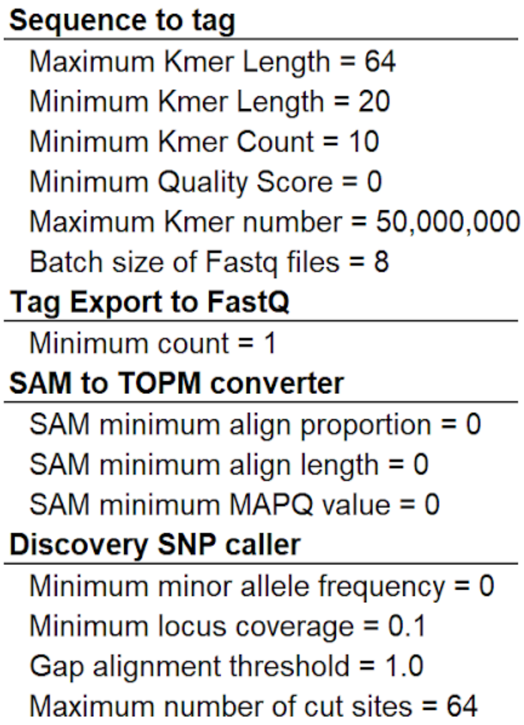
512210NZealand	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Ames30080	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Ames30083	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Ames30084	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Arg1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Arg2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Bol1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Bol2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
bolquestion	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
CR2299colo	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
CR2300Colom	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Ecualf2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Ecualf3	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
GuatUSDA1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
GuatUSDA2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Lamay	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Panalf1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Panalf5	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Panalfg4	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
Peru1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
PI162778	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous
NGB162411Boleracea	*Brassica oleracea*	Northern Europe	Broccoli
PI426177	*B. rapa* Afghanistan	South Asia	Oilseed
PI254544	*B. rapa* Afghanistan, Kabul	South Asia	Oilseed
PI179849	*B. rapa* India	South Asia	Oilseed
PI352809	*B. rapa* India	South Asia	Oilseed
PI352810	*B. rapa* India	South Asia	Oilseed
PI352811	*B. rapa* India	South Asia	Oilseed

PI352822	*B. rapa* India	South Asia	Oilseed
PI352824	*B. rapa* India	South Asia	Oilseed
PI352825	*B. rapa* India	South Asia	Oilseed
PI370737	*B. rapa* India	South Asia	Oilseed
PI603020	*B. rapa* India	South Asia	Oilseed
PI649160	*B. rapa* India	South Asia	Oilseed
PI215578	*B. rapa* India, Bihar	South Asia	Oilseed
PI163496	*B. rapa* India, Punjab	South Asia	Oilseed
PI179641	*B. rapa* India, Punjab	South Asia	Oilseed
PI164841	*B. rapa* India, Uttar Pradesh	South Asia	Oilseed
PI165608	*B. rapa* India, Uttar Pradesh	South Asia	Oilseed
PI175052	*B. rapa* India, Uttar Pradesh	South Asia	Oilseed
PI175054	*B. rapa* India, Uttar Pradesh	South Asia	Oilseed
PI175088	*B. rapa* India, Uttar Pradesh	South Asia	Oilseed
PI175096	*B. rapa* India, Uttar Pradesh	South Asia	Oilseed
PI175066	*B. rapa* Nepal	South Asia	Oilseed
PI250136	*B. rapa* Pakistan	South Asia	Oilseed
PI426234	*B. rapa* Pakistan	South Asia	Oilseed
PI426236	*B. rapa* Pakistan	South Asia	Oilseed
PI426247	*B. rapa* Pakistan	South Asia	Oilseed
PI426248	*B. rapa* Pakistan	South Asia	Oilseed
PI426249	*B. rapa* Pakistan	South Asia	Oilseed
PI426252	*B. rapa* Pakistan	South Asia	Oilseed
PI537013	*B. rapa* Pakistan	South Asia	Oilseed
PI537020	*B. rapa* Pakistan	South Asia	Oilseed
PI603022	*B. rapa* Pakistan	South Asia	Oilseed
PI603023	*B. rapa* Pakistan	South Asia	Oilseed
PI603024	*B. rapa* Pakistan	South Asia	Oilseed
PI633155	*B. rapa* Pakistan	South Asia	Oilseed
PI649164	*B. rapa* Pakistan	South Asia	Oilseed
PI217933	*B. rapa* Pakistan, North-West Front	South Asia	Oilseed
PI217931	*B. rapa* Pakistan, Punjab	South Asia	Oilseed
BRA3039ladakh	*B. rapa* ssp. *trilocularis*	South Asia	Oilseed
CR2672Yemen	*B. rapa* ssp. *trilocularis*	South Asia	Oilseed
PI351823	*B. rapa* ssp. *trilocularis*	South Asia	Oilseed
PI662679	*B. rapa* subsp. *chinensis* Japan	South Asia	Oilseed
PI347594	*B. rapa* subsp. *dichotoma* India	South Asia	Oilseed
PI347602	*B. rapa* subsp. *dichotoma* India	South Asia	Oilseed
PI649168	*B. rapa* subsp. *dichotoma* India	South Asia	Oilseed
PI649173	*B. rapa* subsp. *dichotoma* India	South Asia	Oilseed

PI649178	*B. rapa* subsp. *dichotoma* India	South Asia	Oilseed
PI662642	*B. rapa* subsp. *dichotoma* India	South Asia	Oilseed
PI633166	*B. rapa* subsp. *dichotoma* Nepal	South Asia	Oilseed
PI649181	*B. rapa* subsp. *dichotoma* U.S. Iowa	South Asia	Oilseed
PI649194	*B. rapa* subsp. *oleifera* Germany	South Asia	Oilseed
G30623	*B. rapa* subsp. *oleifera* India	South Asia	Oilseed
PI508415	*B. rapa* subsp. *pekinensis* South Korea	South Asia	Oilseed
PI346882	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI347608	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI459016	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI459019	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI459020	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI459021	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI459023	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI649198	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI649199	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI649200	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI649201	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI649202	*B. rapa* subsp. *trilocularis* India	South Asia	Oilseed
PI390142	*B. rapa* subsp. *trilocularis* Pakistan	South Asia	Oilseed
PI426420	*B. rapa* subsp. *trilocularis* Pakistan	South Asia	Oilseed
PI426422	*B. rapa* subsp. *trilocularis* Pakistan	South Asia	Oilseed
PI426423	*B. rapa* subsp. *trilocularis* Pakistan	South Asia	Oilseed
PI649204	*B. rapa* subsp. *trilocularis* U.S. Iowa	South Asia	Oilseed
PI649206	*B. rapa* subsp. *trilocularis* U.S. Iowa	South Asia	Oilseed
PI649207	*B. rapa* subsp. *trilocularis* U.S. Iowa	South Asia	Oilseed

PI649208	*B. rapa* subsp. *trilocularis* U.S. Iowa	South Asia	Oilseed
PI179863	*B. rapa* India, Uttar Pradesh	Sw Asia	Turnip
PI179189	*B. rapa* Iraq	Sw Asia	Turnip
BRA1717TajikT	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
BRA1901TIraq	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
BRA2196Turkey	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
BRA2985Tajik	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI125797TAfg	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI125798TAfg	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI127440TAfg	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI138894TIran	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI169061TTur	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI169064balikesir	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI169070TTur	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI177286hakkari	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI183664TTur	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI211582TAfg	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI222236TIran	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI268368TAfg	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI269439TPak	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
PI269441TPak	*B. rapa* ssp. *rapa*	Sw Asia	Turnip
GeorgiaBRA1716	*B. rapa* ssp. *rapa*	Sw Asia	Turnip

Supplementary material 2. Tassel 5 GBS 2 pipeline parameters used.



Sequence to tag

Maximum Kmer Length = 64
Minimum Kmer Length = 20
Minimum Kmer Count = 10
Minimum Quality Score = 0
Maximum Kmer number = 50,000,000
Batch size of Fastq files = 8

Tag Export to FastQ

Minimum count = 1

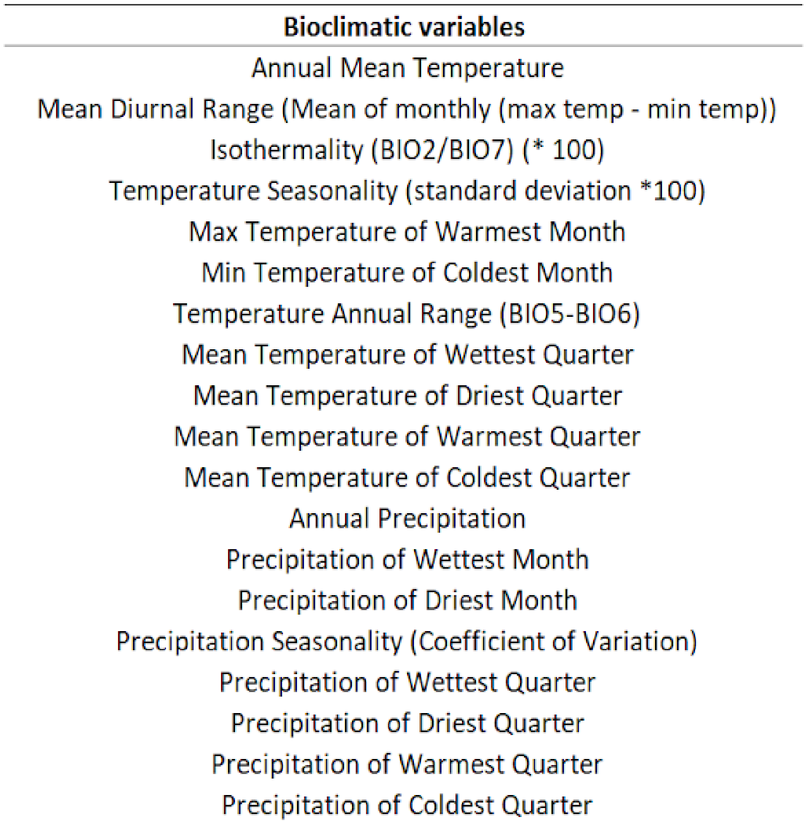
SAM to TOPM converter

SAM minimum align proportion = 0
SAM minimum align length = 0
SAM minimum MAPQ value = 0

Discovery SNP caller

Minimum minor allele frequency = 0
Minimum locus coverage = 0.1
Gap alignment threshold = 1.0
Maximum number of cut sites = 64

Supplementary material 3. Bioclimatic variables used for niche modeling



Bioclimatic variables
Annual Mean Temperature
Mean Diurnal Range (Mean of monthly (max temp - min temp))
Isothermality (BIO2/BIO7) (* 100)
Temperature Seasonality (standard deviation *100)
Max Temperature of Warmest Month
Min Temperature of Coldest Month
Temperature Annual Range (BIO5-BIO6)
Mean Temperature of Wettest Quarter
Mean Temperature of Driest Quarter
Mean Temperature of Warmest Quarter
Mean Temperature of Coldest Quarter
Annual Precipitation
Precipitation of Wettest Month
Precipitation of Driest Month
Precipitation Seasonality (Coefficient of Variation)
Precipitation of Wettest Quarter
Precipitation of Driest Quarter
Precipitation of Warmest Quarter
Precipitation of Coldest Quarter

Supplementary material 4. Samples used for genotyping-by-sequencing in chapter 3.

Sample name/accession number	**Subspecies and location information**	**Geographic region**	**Crop type**	**Dataset**
M143grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M163grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M173grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M190grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M197grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M316grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M417grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M472grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A

M588grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M599grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
M82grelo	*B. rapa* subsp. *sylvestris* var. esculenta	Europe	Grelos	A
PI662684	*B. rapa* Italy	Europe	Rapini	A
PI633161	*B. rapa* Italy, Calabria	Europe	Rapini	A
PI633168	*B. rapa* subsp. *oleifera* Italy	Europe	Rapini	A
PI662794	*B. rapa* subsp. *oleifera* Italy	Europe	Rapini	A
PI662685	*B. rapa* subsp. *rapa* Italy	Europe	Rapini	A
PI662683	*B. rapa* U.S.	Europe	Rapini	A
bavicquar	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini	A
bavinccentoventesta	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini	A
bavincnoventina	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini	A
bavincricamrzno	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini	A
CR2551italian	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini	A
PI6331680Italy	*B. rapa* ssp. *sylvestris* var. esculenta	Europe	Rapini	A
BR50227cuenc	*B. rapa* ssp. *rapa*	Europe	Spanish turnip	A
BRA2218Canada	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous	A
Quebecemilyharvest	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous	A
Quebecsimard2	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous	A
Simard3WCanada	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous	A
TN2974QuebecMilby	*B. rapa* ssp. *sylvestris*	Canada	Spontaneous	A
BRA2809Turk	*B. rapa* ssp. *sylvestris*	Caucusus	Spontaneous	A
Cr2211geor	*B. rapa* ssp. *sylvestris*	Caucusus	Spontaneous	A
CR2234Russiasilv	*B. rapa* ssp. *sylvestris*	Caucusus	Spontaneous	A
CR2241georg	*B. rapa* ssp. *sylvestris*	Caucusus	Spontaneous	A
CR2269senzatesta	*B. rapa* ssp. *sylvestris*	Caucusus	Spontaneous	A
CR2354georg	*B. rapa* ssp. *sylvestris*	Caucusus	Spontaneous	A
Georgiahoney	*B. rapa* ssp. *sylvestris*	Caucusus	Spontaneous	A
PI198061	*B. rapa* Sweden	Europe	Spontaneous	A
PI360878	*B. rapa* Sweden	Europe	Spontaneous	A
PI649162	*B. rapa* Sweden	Europe	Spontaneous	A
BRA2465sweden	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
CR1538OSlovakia	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
CR1578slovak	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
CR2210slovak	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A

CR2213austria	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
CR2355Britain	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
Ewijk	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
GaliniMaarsen	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
Lindbjerg	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
Lonstorp	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
NGB1320661Horne	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
NGB1320671Branbjerg	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
NGB132068.1WOutrup	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
PI537003Serb	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
Wageningen	*B. rapa* ssp. *sylvestris*	Europe	Spontaneous	A
PI250004	*B. rapa* Egypt	Africa	Turnip	A
BRA1718TLibya	*B. rapa* ssp. *rapa*	Africa	Turnip	A
CR2552OLibya	*B. rapa* ssp. *rapa*	Africa	Turnip	A
G31848	*B. rapa* Germany	Europe	Turnip	A
PI662772	*B. rapa* Germany	Europe	Turnip	A
BR50226valenc	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRS0225Valenc	*B. rapa* ssp. *rapa*	Europe	Turnip	A
EXTBRS0228TCastellon	*B. rapa* ssp. *rapa*	Europe	Turnip	A
EXTBRSO231Caceres	*B. rapa* ssp. *rapa*	Europe	Turnip	A
EXTBRSO239Santander	*B. rapa* ssp. *rapa*	Europe	Turnip	A
PI662694	*B. rapa* subsp. *rapa* France	Europe	Turnip	A
G31841	*B. rapa* subsp. *rapa* Germany	Europe	Turnip	A
PI662795	*B. rapa* subsp. *rapa* Netherlands	Europe	Turnip	A
G30808	*B. rapa* subsp. *rapa* U.S.	Europe	Turnip	A
PI662692	*B. rapa* subsp. *rapa* U.S.	Europe	Turnip	A
PI662775	*B. rapa* subsp. *rapa* Unknown	Europe	Turnip	A
PI662773	*B. rapa* Unknown	Europe	Turnip	A
PI662774	*B. rapa* Unknown	Europe	Turnip	A
PI662780	*B. rapa* Unknown	Europe	Turnip	A
PI662781	*B. rapa* Unknown	Europe	Turnip	A
175608takirdag	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRA1018TAustria	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRA1709TTunisian	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRA1831TItaly	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRA1892TGeorgia	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRA1894TItaly	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRA2731TItaly	*B. rapa* ssp. *rapa*	Europe	Turnip	A
BRA917THungary	*B. rapa* ssp. *rapa*	Europe	Turnip	A
CR1542OPoland	*B. rapa* ssp. *rapa*	Europe	Turnip	A
PI169082samsun	*B. rapa* ssp. *rapa*	Europe	Turnip	A

PI633178TDenmark	*B. rapa* ssp. *rapa*	Europe	Turnip	A
PI649185OGermany	*B. rapa* ssp. *rapa*	Europe	Turnip	A
PI649189Belgium	*B. rapa* ssp. *rapa*	Europe	Turnip	A
questionFinlandBRA1814	*B. rapa* ssp. *rapa*	Europe	Turnip	A
questionYugoBRA2780	*B. rapa* ssp. *rapa*	Europe	Turnip	A
Rejogochib9	*B. rapa* ssp. *rapa*	Europe	Turnip	A
PI179863	*B. rapa* India, Uttar Pradesh	S/C Asia	Turnip	A
PI179189	*B. rapa* Iraq	S/C Asia	Turnip	A
BRA1717TajikT	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
BRA1901TIraq	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
BRA2196Turkey	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
BRA2985Tajik	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI125797TAfg	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI125798TAfg	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI127440TAfg	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI138894TIran	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI169061TTur	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI169064balikesir	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI169070TTur	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI177286hakkari	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI183664TTur	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI211582TAfg	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI222236TIran	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI268368TAfg	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI269439TPak	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
PI269441TPak	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
GeorgiaBRA1716	*B. rapa* ssp. *rapa*	S/C Asia	Turnip	A
NGB162411Boleracea	*Brassica oleracea*	Northern Europe	Broccoli	A
PI204683Kayseri	*B. rapa* ssp. *rapa* Turkey	Latin America	Spontaneous	A/B
14Alej46a	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
14Alej46c	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
14Alej47	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
14Alej62	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
14DFmark11b	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
14Pan59	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
14Pan61b	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B

2Colpos1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
3Colpos2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
3Colpos3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
AboveChuneloatfield4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
AboveChuneloatfield5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
AboveChuneloatfield6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
AboveChuneloatfield7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Alejf1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Alejf2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Alejf3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Alejf4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Alejf5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Analco8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ang8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Berta1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Berta2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Bneigh1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Bneigh2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B

Bneighc	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Celiabawino1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Celiabawino2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Celiabawino3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Celiabawino4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Choguitaavena1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Choguitaworkshopb2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Choguitaworkshopb3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Choguitaworkshopb4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Choguitaworkshopb5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Choguitaworkshopb6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Claudia1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Claudia2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cocham10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cochararehouse1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cochararehouse2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cochararemilpa1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cochararemilpa2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cochararemilpa3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cochararemilpa4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Cocheram2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Creel3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Creel4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
espinaca10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
espinaca5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B

espinaca6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
espinaca7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
espinaca8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
espinaca9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
EspinacaB1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
EspinacaB2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
EspinacaB3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
EspinacaB4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
InoatfieldRanchoblanco1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
InoatfieldRanchoblanco2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
InoatfieldRanchoblanco3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
InoatfieldRanchoblanco4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
IntownSanJuanito1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Jim1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
lupeworkshop1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Margar1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Margar2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariomilpa1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariomilpa3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariomilpa4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariomilpa6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariomilpa7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Marioseedbankb10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Marioseedbankb5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Marioseedbankb6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B

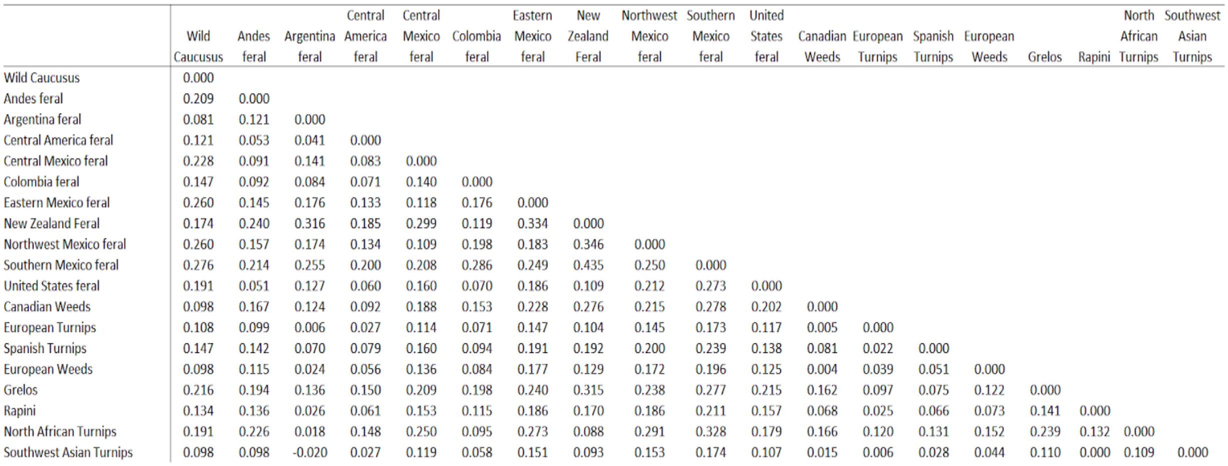
Marioseedbankb7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Marioseedbankb8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Marioseedbankb9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariosembrado1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariosembrado2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariosembrado3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Mariosembrado4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho20071	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho20072	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho20073	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho20074	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho2007b5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho2007b6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho2007b7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Nacho2007b8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ozumbacriollo1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ranchoblanco13	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ranchoblanco2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ranchoblanco5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ranchoblanco6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ranchoblanco7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Ranchoblanco9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu11	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu12	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B

Refu2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu25	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refu9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refugio2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Refugio3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejo1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejo2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejo3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejo4	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejogochib10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejogochib5	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejogochib6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejogochib7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Rejogochib8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Sanignacmb10	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Sanignacmb6	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Sanignacmb7	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Sanignacmb8	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Sanignacmb9	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B

Santiag1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Santiag2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Santiag3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Sisoguichi1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Vainooo1	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Vainooo2	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
Vainooo3	*B. rapa* ssp. *sylvestris* Mexico	Latin America	Spontaneous	A/B
PI633181	*B. rapa* subsp. *rapa* Honduras, Lempira	Latin America	Spontaneous	A/B
311711Chile	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
512210NZealand	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Ames30080	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Ames30083	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Ames30084	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Arg1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Arg2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Bol1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Bol2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
bolquestion	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
CR2299colo	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
CR2300Colom	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Ecualf2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Ecualf3	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
GuatUSDA1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
GuatUSDA2	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Lamay	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B

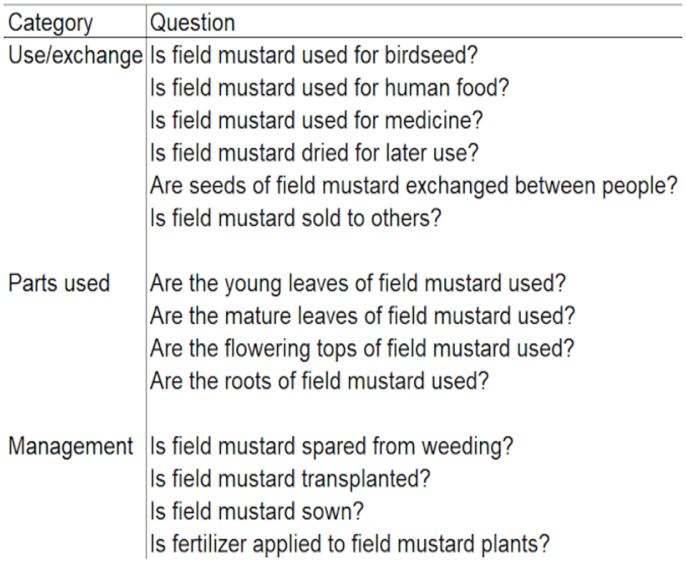
Panalf1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Panalf5	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Panalfg4	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
Peru1	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B
PI162778	*B. rapa* ssp. *sylvestris*	Latin America	Spontaneous	A/B

Supplementary material 5. F_{ST} index values comparing populations in dataset A of chapter 3.



	Wild Caucusus	Andes feral	Argentina feral	Central America feral	Central Mexico feral	Colombia feral	Eastern Mexico feral	New Zealand Feral	Northwest Mexico feral	Southern Mexico feral	United States feral	Canadian Weeds	European Turnips	Spanish Turnips	European Weeds	Grelos	Rapini	North African Turnips	Southwest Asian Turnips
Wild Caucusus	0.000																		
Andes feral	0.209	0.000																	
Argentina feral	0.081	0.121	0.000																
Central America feral	0.121	0.053	0.041	0.000															
Central Mexico feral	0.228	0.091	0.141	0.083	0.000														
Colombia feral	0.147	0.092	0.084	0.071	0.140	0.000													
Eastern Mexico feral	0.260	0.145	0.176	0.133	0.118	0.176	0.000												
New Zealand Feral	0.174	0.240	0.316	0.185	0.299	0.119	0.334	0.000											
Northwest Mexico feral	0.260	0.157	0.174	0.134	0.109	0.198	0.183	0.346	0.000										
Southern Mexico feral	0.276	0.214	0.255	0.200	0.208	0.286	0.249	0.435	0.250	0.000									
United States feral	0.191	0.051	0.127	0.060	0.160	0.070	0.186	0.109	0.212	0.273	0.000								
Canadian Weeds	0.098	0.167	0.124	0.092	0.188	0.153	0.228	0.276	0.215	0.278	0.202	0.000							
European Turnips	0.108	0.099	0.006	0.027	0.114	0.071	0.147	0.104	0.145	0.173	0.117	0.005	0.000						
Spanish Turnips	0.147	0.142	0.070	0.079	0.160	0.094	0.191	0.192	0.200	0.239	0.138	0.081	0.022	0.000					
European Weeds	0.098	0.115	0.024	0.056	0.136	0.084	0.177	0.129	0.172	0.196	0.125	0.004	0.039	0.051	0.000				
Grelos	0.216	0.194	0.136	0.150	0.209	0.198	0.240	0.315	0.238	0.277	0.215	0.162	0.097	0.075	0.122	0.000			
Rapini	0.134	0.136	0.026	0.061	0.153	0.115	0.186	0.170	0.186	0.211	0.157	0.068	0.025	0.066	0.073	0.141	0.000		
North African Turnips	0.191	0.226	0.018	0.148	0.250	0.095	0.273	0.088	0.291	0.328	0.179	0.166	0.120	0.131	0.152	0.239	0.132	0.000	
Southwest Asian Turnips	0.098	0.098	-0.020	0.027	0.119	0.058	0.151	0.093	0.153	0.174	0.107	0.015	0.006	0.028	0.044	0.110	0.000	0.109	0.000

Supplementary material 6. Structured survey questions used in chapter 4.



Category	Question
Use/exchange	Is field mustard used for birdseed?
	Is field mustard used for human food?
	Is field mustard used for medicine?
	Is field mustard dried for later use?
	Are seeds of field mustard exchanged between people?
	Is field mustard sold to others?
Parts used	Are the young leaves of field mustard used?
	Are the mature leaves of field mustard used?
	Are the flowering tops of field mustard used?
	Are the roots of field mustard used?
Management	Is field mustard spared from weeding?
	Is field mustard transplanted?
	Is field mustard sown?
	Is fertilizer applied to field mustard plants?

Supplementary material 7. Example questions for semi-structured interviews and focus groups in chapter 4.

What is field mustard used for?
What parts of field mustard are used?
How is field mustard prepared
Is field mustard planted?
    - Are any allowed to go to seed?
    - How are seeds chosen to plant each year?
    - Where do the seeds come from?
    - Are they planted alone or with other plants?

Do people collect field mustard that grows on its own?
    - Where do they grow?

Do people sell field mustard?
    - How much do people harvest?
    - How much is it sold for?

How long have people in this area been using field mustard?
Are people using field mustard, more, less, or the same amount as in the past?

Supplementary material 8. Samples included in chapter 5

Sample	Population	Population code
Celiabawino1	bahuinocachi_wild	BAW_W1
Celiabawino2	bahuinocachi_wild	BAW_W1
Celiabawino3	bahuinocachi_wild	BAW_W1
Celiabawino4	bahuinocachi_wild	BAW_W1
Choguitaworkshopb2	choguita_managed	CHO_M2
Choguitaworkshopb4	choguita_managed	CHO_M2
Choguitaworkshopb5	choguita_managed	CHO_M2
Choguitaworkshopb6	choguita_managed	CHO_M2
lupeworkshop1	choguita_managed	CHO_M2
espinaca10	cocharare_managed	COC_M5
espinaca5	cocharare_managed	COC_M5
espinaca6	cocharare_managed	COC_M5
espinaca7	cocharare_managed	COC_M5
espinaca8	cocharare_managed	COC_M5
espinaca9	cocharare_managed	COC_M5
EspinacaB1	cocharare_managed	COC_M5
EspinacaB2	cocharare_managed	COC_M5
EspinacaB3	cocharare_managed	COC_M5
EspinacaB4	cocharare_managed	COC_M5
Cocham10	cocharare_wild	COC_W4
Cochararehouse1	cocharare_wild	COC_W4
Cochararehouse2	cocharare_wild	COC_W4
Cochararemilpa1	cocharare_wild	COC_W4
Cochararemilpa2	cocharare_wild	COC_W4
Cochararemilpa3	cocharare_wild	COC_W4
Cochararemilpa4	cocharare_wild	COC_W4
Cocheram2	cocharare_wild	COC_W4
Marioseedbankb10	gumisachi_managed	GUM_M1
Marioseedbankb5	gumisachi_managed	GUM_M1
Marioseedbankb6	gumisachi_managed	GUM_M1
Marioseedbankb7	gumisachi_managed	GUM_M1
Marioseedbankb8	gumisachi_managed	GUM_M1
Marioseedbankb9	gumisachi_managed	GUM_M1
Mariosembrado1	gumisachi_managed	GUM_M1
Mariosembrado2	gumisachi_managed	GUM_M1
Mariosembrado3	gumisachi_managed	GUM_M1
Mariosembrado4	gumisachi_managed	GUM_M1
Mariomilpa1	gumisachi_wild	GUM_W5
Mariomilpa3	gumisachi_wild	GUM_W5
Mariomilpa4	gumisachi_wild	GUM_W5
Mariomilpa6	gumisachi_wild	GUM_W5
Mariomilpa7	gumisachi_wild	GUM_W5

AboveChuneloatfield4	norogachi_wild	NOR_W2
AboveChuneloatfield5	norogachi_wild	NOR_W2
AboveChuneloatfield6	norogachi_wild	NOR_W2
AboveChuneloatfield7	norogachi_wild	NOR_W2
Refu1	panalache_managed	PAN_M3
Refu11	panalache_managed	PAN_M3
Refu12	panalache_managed	PAN_M3
Refu2	panalache_managed	PAN_M3
Refu25	panalache_managed	PAN_M3
Refu3	panalache_managed	PAN_M3
Refu4	panalache_managed	PAN_M3
Refu5	panalache_managed	PAN_M3
Refu6	panalache_managed	PAN_M3
Refu7	panalache_managed	PAN_M3
Refu8	panalache_managed	PAN_M3
Refu9	panalache_managed	PAN_M3
Refugio2	panalache_managed	PAN_M3
Refugio3	panalache_managed	PAN_M3
14Pan59	panalache_wild	PAN_W6
14Pan61b	panalache_wild	PAN_W6
Jim1	panalache_wild	PAN_W6
Nacho20071	panalache_wild	PAN_W6
Nacho20072	panalache_wild	PAN_W6
Nacho20073	panalache_wild	PAN_W6
Nacho20074	panalache_wild	PAN_W6
Nacho2007b5	panalache_wild	PAN_W6
Nacho2007b6	panalache_wild	PAN_W6
Nacho2007b7	panalache_wild	PAN_W6
Nacho2007b8	panalache_wild	PAN_W6
InoatfieldRanchoblanco1	rancho_blanco_wild	RAN_W3
InoatfieldRanchoblanco2	rancho_blanco_wild	RAN_W3
InoatfieldRanchoblanco3	rancho_blanco_wild	RAN_W3
InoatfieldRanchoblanco4	rancho_blanco_wild	RAN_W3
Ranchoblanco13	rancho_blanco_wild	RAN_W3
Ranchoblanco2	rancho_blanco_wild	RAN_W3
Ranchoblanco5	rancho_blanco_wild	RAN_W3
Ranchoblanco6	rancho_blanco_wild	RAN_W3
Ranchoblanco7	rancho_blanco_wild	RAN_W3
Ranchoblanco9	rancho_blanco_wild	RAN_W3
Rejo1	rejogochi_wild	REJ_W7
Rejo2	rejogochi_wild	REJ_W7
Rejo3	rejogochi_wild	REJ_W7
Rejogochib10	rejogochi_wild	REJ_W7
Rejogochib5	rejogochi_wild	REJ_W7
Rejogochib6	rejogochi_wild	REJ_W7
Rejogochib7	rejogochi_wild	REJ_W7
Rejogochib8	rejogochi_wild	REJ_W7
Alejf2	san_ignacio_managed	SAN_M4
Alejf3	san_ignacio_managed	SAN_M4
Alejf4	san_ignacio_managed	SAN_M4
Alejf5	san_ignacio_managed	SAN_M4
Alejf1	san_ignacio_managed	SAN_M4
14Alej46a	san_ignacio_wild	SAN_W8
14Alej46c	san_ignacio_wild	SAN_W8
14Alej47	san_ignacio_wild	SAN_W8
14Alej62	san_ignacio_wild	SAN_W8
Sanignacmb10	san_ignacio_wild	SAN_W8
Sanignacmb6	san_ignacio_wild	SAN_W8
Sanignacmb7	san_ignacio_wild	SAN_W8
Sanignacmb8	san_ignacio_wild	SAN_W8
Sanignacmb9	san_ignacio_wild	SAN_W8

Supplementary material 9. Parameters and residuals of optimal demographic model in chapter 2.

Parameters

Genetic units are given by nu for population sizes (scaled against ancestral Ne), T in units of 2N generations (from present), and migration rates m in 2Nm (per generation) units.

nu_ancestral = 1

nu_cau = 0.08

T_cau (time caucasus shrunk in size) = 0.017

T_split (caucasus with turnips) = 0.048

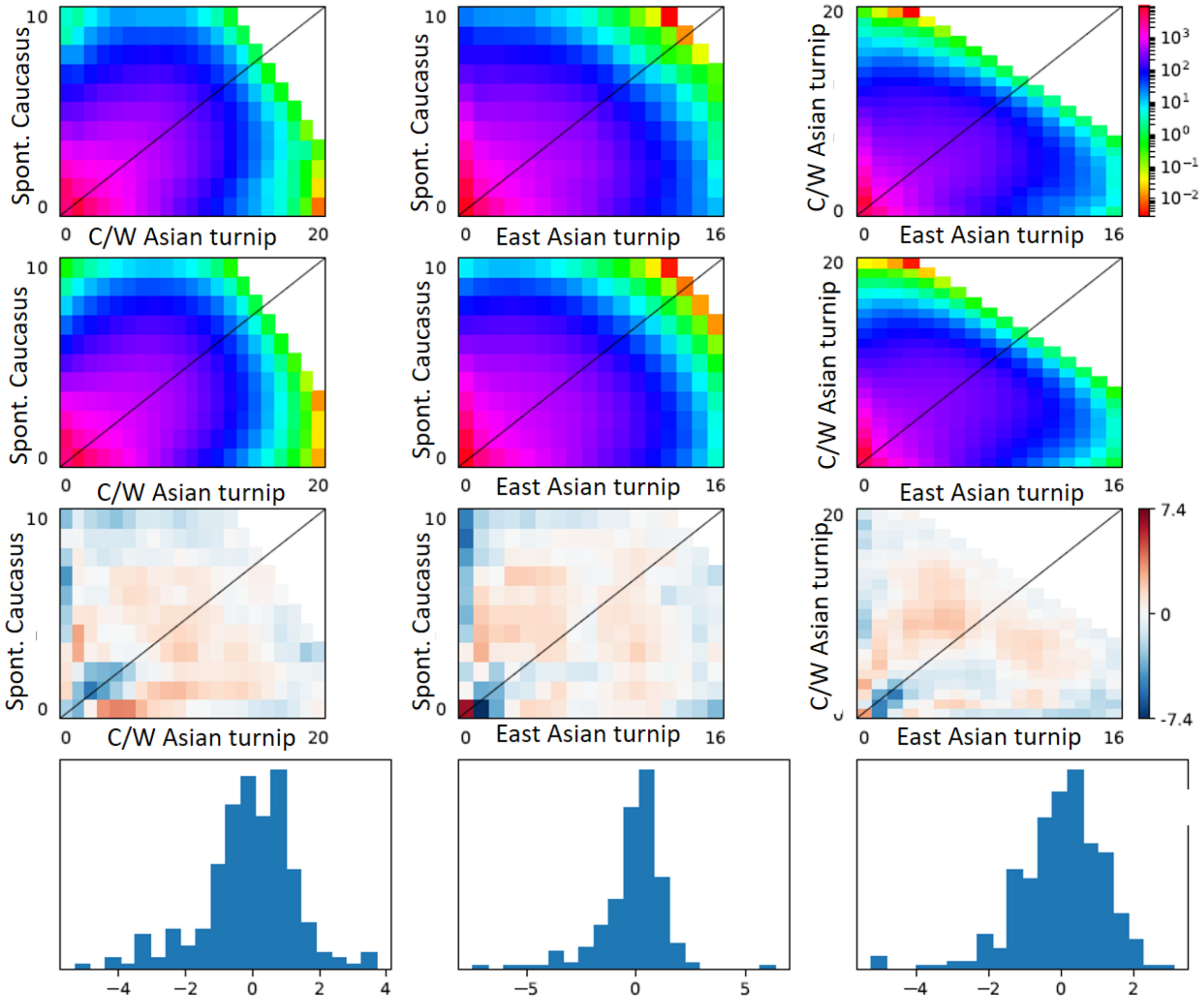
T_split (between turnips) = 0.016

m (out of wild caucasus) = 26

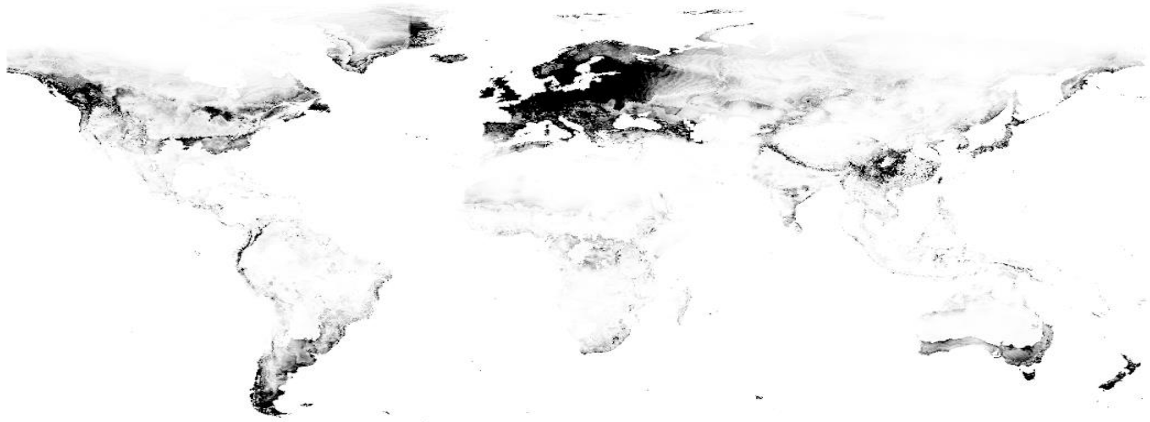
m (out of turnips) = 13

Residuals

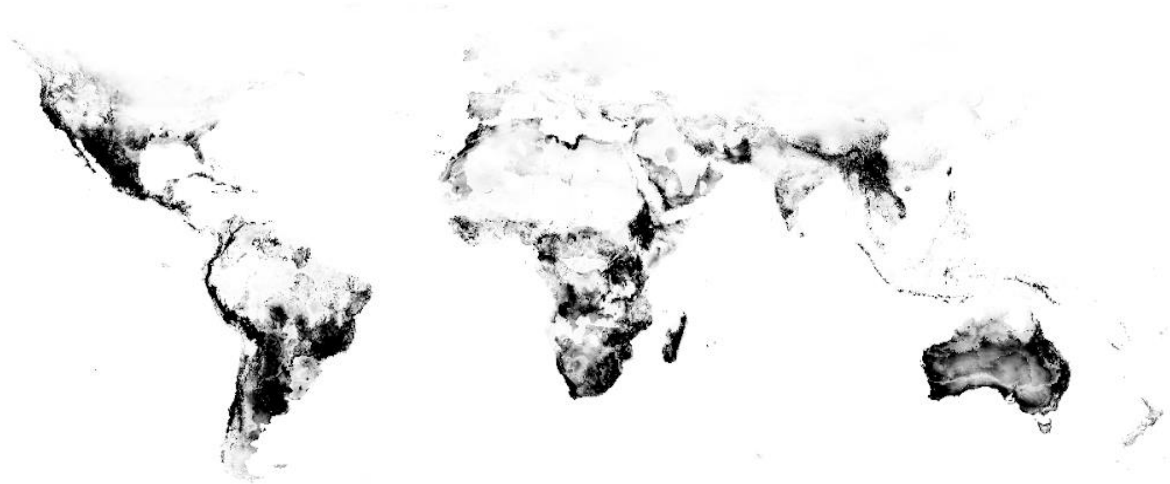
The top row represents the data, the second row is the model, the third row are residuals (model-data), and the bottom row are a histogram of all residuals.


Spont. Caucasus
C/W Asian turnip
East Asian turnip
C/W Asian turnip
0
10
20
16
10^3
10^2
10^1
10^0
10^{-1}
10^{-2}
7.4
0
-7.4
−4
−2
0
2
4
−5
5

Supplementary material 9. Species distribution models for chapter 3 of spontaneously occurring *B. rapa* trained on occurrence data from A) the putative native range in Eurasia and B), the invaded range of Latin America



A.



B.

Supplementary materials 10. Global occurrence data for *Brassica rapa* from GBIF.org (Accessed February 2, 2018).