Check for updates

Received: 17 January 2022 | Accepted: 30 August 2022

DOI: 10.1002/ajb2.16090

SPECIAL ISSUE ARTICLE

Botany

The *Boechera* model system for evolutionary ecology

Catherine A. Rushworth[1] | **Maggie R. Wagner**[2] | **Thomas Mitchell-Olds**[3] | **Jill T. Anderson**[4]

[1]Department of Biology, Utah State University, Logan, UT 84322, USA

[2]Department of Ecology and Evolutionary Biology, Kansas Biological Survey and Center for Ecological Research, University of Kansas, Lawrence, KS 66045, USA

[3]Department of Biology, Duke University, Box 90338, Durham, NC 27708, USA

[4]Department of Genetics and Odum School of Ecology, University of Georgia, Athens, GA 30602, USA

Correspondence

Jill T. Anderson, Department of Genetics and Odum School of Ecology, University of Georgia, Athens, GA 30602, USA.
Email: jta24@uga.edu

Thomas Mitchell-Olds, Department of Biology, Duke University, Box 90338, Durham, NC 27708, USA.
Email: tmo1@duke.edu

Abstract

Model systems in biology expand the research capacity of individuals and the community. Closely related to *Arabidopsis*, the genus *Boechera* has emerged as an important ecological model owing to the ability to integrate across molecular, functional, and eco-evolutionary approaches. *Boechera* species are broadly distributed in relatively undisturbed habitats predominantly in western North America and provide one of the few experimental systems for identification of ecologically important genes through genome-wide association studies and investigations of selection with plants in their native habitats. The ecologically, evolutionarily, and agriculturally important trait of apomixis (asexual reproduction via seeds) is common in the genus, and field experiments suggest that abiotic and biotic environments shape the evolution of sex. To date, population genetic studies have focused on the widespread species *B. stricta*, detailing population divergence and demographic history. Molecular and ecological studies show that balancing selection maintains genetic variation in ~10% of the genome, and ecological trade-offs contribute to complex trait variation for herbivore resistance, flowering phenology, and drought tolerance. Microbiome analyses have shown that host genotypes influence leaf and root microbiome composition, and the soil microbiome influences flowering phenology and natural selection. Furthermore, *Boechera* offers numerous opportunities for investigating biological responses to global change. In *B. stricta*, climate change has induced a shift of >2 weeks in the timing of first flowering since the 1970s, altered patterns of natural selection, generated maladaptation in previously locally-adapted populations, and disrupted life history trade-offs. Here we review resources and results for this eco-evolutionary model system and discuss future research directions.

KEYWORDS

apomixis, *Boechera*, Brassicaceae, climate change, ecology, glucosinolate, local adaptation, selection

Model systems in biology have yielded important insights into fundamental developmental and cellular processes, and the genetic basis of phenotypic traits (e.g., Gasch et al., 2016; Goldstein and King, 2016). These systems, including *Arabidopsis thaliana*, are typically short-lived, easy to cultivate in the laboratory, and amenable to numerous experimental manipulations and genetic transformations. Nevertheless, model systems represent a limited diversity of form and function and cannot answer critical research questions that apply to a diversity of species with different life histories, geographic distributions, symbioses, or evolutionary histories (Goldstein and King, 2016). For example, the annual species *A. thaliana* would not be appropriate for investigating issues pertaining to perennial species, such as resource allocation to current vs. future reproduction under different environmental contexts (Williams, 1966; Bell, 1980; Obeso, 2002; Sletvold and Ågren, 2015) or the extent to which interannual temporal variation in conditions influences the evolution of adaptive plasticity in long-lived species in which individuals can experience multiple years of heterogeneous conditions (Van Kleunen et al., 2007; Wagner and Mitchell-Olds, 2018; Anderson et al., 2021). Furthermore, studies that exclusively occur in laboratory settings with traditional model systems lack the ecological

This article is part of the *AJB* Special Issue "Approaches to the Study of Quantitative Fitness-Related Traits."

 © 2022 Botanical Society of America.

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

relevance to inform our understanding of how multiple abiotic and biotic factors drive evolution in complex natural environments. In recent decades, field studies of model systems like *A. thaliana* have leveraged genetic and molecular tools developed in the laboratory to investigate evolutionary dynamics in nature (e.g., Brachi et al., 2010; Wilczek et al., 2014; Exposito-Alonso et al., 2019b; Ellis et al., 2021). Similarly, biologists have developed other taxa as emerging model systems for addressing eco-evolutionary research questions in realistic field environments in which these species evolved (Table 1). Such ecological models include species with broader variation in ecologies and evolutionary histories than genetic model systems.

Researchers developing entirely new systems often struggle to propagate plants for field and laboratory experiments and confront other challenges that arise from limited resources. In contrast, ecological model species typically offer advantages, including communities of researchers with expertise in experimental manipulations, genetic and genomic studies, and functional trait analysis. Here, we highlight key advances and emerging areas of inquiry that have been made in *Boechera* (Brassicaceae), an experimentally tractable genus that is suitable for field and laboratory experiments. We illustrate how species in this genus can shed light on key biological questions, such as the evolution of apomixis, the genetic architecture of complex traits, the ecology and evolution of biotic interactions, the importance of phenotypic plasticity, and the responses of natural populations to global change (Figure 1).

Why *Boechera*?

The genus *Boechera* (Brassicaceae) is a relatively new addition to ecological model systems and offers several key benefits. First, its native range in relatively undisturbed sites across western North America (Alexander et al., 2013; Li et al., 2017), where the climate is changing rapidly (Mountain Research Initiative, 2015; Fyfe et al., 2017) provides opportunities for ecological work across steep environmental gradients spanning short geographic distances, with immediate relevance to climate change work. Experiments in such complex natural environments can address fundamental and emerging questions at the intersection of ecology, evolution, and genetics. *Boechera* has been developed as an eco-evolutionary model system, owing in part to its relatedness to *Arabidopsis*, such that molecular tools, synteny, annotations, and information regarding gene function are readily transferable. Its close relationship with *Capsella*, a model system in evolutionary and population genetics (Lafon-Placette et al., 2018; Koenig et al., 2019; Dziasek et al., 2021), enables comparative work across the Brassicaceae. Genome sequences and annotations are now available for *B. stricta*, *B. retrofracta*, *B. fecunda*, and some apomictic hybrids (Lee et al., 2017; Lovell et al., 2017; Kliver et al., 2018; Zhang et al., 2020).

The perennial nature of some *Boechera* species enables researchers to examine temporal variation in trait expression and selection (Wadgymar et al., 2017), and fitness trade-offs across episodes of selection (Anderson et al., 2014) and life history stages (Hamann et al., 2021b). *Boechera* balances these advantages against the major downside of perenniality, which is the longer time investment needed to complete experiments. In field experiments many *Boechera* species are short-lived perennials or effectively annual (Rushworth et al., 2020). Thus, large-scale experiments in natural and laboratory environments (Figure 2) can be completed relatively rapidly. Finally, long-term ecological and demographic data sets are available in several *Boechera* species (Wadgymar et al., 2018b; Anderson and Wadgymar, 2020; Carley et al., 2022), addressing questions about conservation biology and biological responses to climate change.

Well-characterized reproductive variation in *Boechera* carries several advantages for experimental work. Most *Boechera* species are tolerant of inbreeding (Song and Mitchell-Olds, 2007), which facilitates genome-wide association studies (GWAS), quantitative trait locus (QTL) mapping, and quantitative genetic experiments. Lineages can be crossed to produce mapping populations, which can be developed relatively quickly because two generations can be grown per year in the greenhouse. Finally, a public domain panel of >400 sequenced *B. stricta* accessions is available, enabling GWAS in *Boechera* (Yan et al., 2021). Thus, interspecific comparison of the genetic architecture of complex traits is feasible between the closely related *A. thaliana* and *B. stricta*. Finally, although hybridization, polyploidy, and apomixis complicate systematics of the group (Beck et al., 2012; Li et al., 2017; Mandáková et al., 2020), interfertility facilitates studies of hybridization and speciation (Alexander et al., 2013). Widespread apomixis in the genus, particularly at the diploid level, permits studies of this important trait in a tractable, diploid system with a small genome (Brukhin et al., 2019).

Apomixis and reproductive ecology

The reproductive ecology of *Boechera* has been well characterized, with numerous studies showing the dominant mode of reproduction is self-fertilization (Roy and Rieseberg 1989; Roy 1995; Song et al. 2006; Rushworth et al., 2011) and apomixis, i.e., the asexual production of seed (Schranz et al., 2005; Beck et al., 2012; Li et al., 2017). In controlled conditions, the high frequency of self-fertilization facilitates formation of inbred lines for genetic work, but traits common in highly self-fertilizing species (the "selfing syndrome," including small flowers and reduced pollen) complicate emasculation and hand-pollination. Seed set of selfing species via autonomous selfing is robust, but controlled selfing results in low seed set (Rushworth and Mitchell-Olds, 2021). Low levels of outcrossing occur even in highly self-fertilizing species, as

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Characteristics of key eco-evolutionary model systems. For each genus, we first list general attributes, including the number of species, whether a phylogeny is available, whether species in the genus are apomictic and whether species have sex chromosomes. We then indicate traits associated with the most commonly studied model species of each genus, general research areas, and a sampling of related publications.

	Genus-level attributes				Traits of primary model species			
Genus	No. of species	Phylogeny[A]	Apomixis[B]	Sexual traits[C]	Model species	Annotated genome[D]	Estimated genome size	Minimum generation time (mo)
Aquilegia	60	Y	S	A	*A. coerulea*	Y	292 Mb	3-4
Arabidopsis	10	Y	S	A	*A. thaliana*	Y	125 Mb	1
Boechera	100+	in progress	X	A	*B. stricta*	Y	197 Mb	6
Brassica	37	Y	S	A	*B. rapa*	Y	443 Mb	1
Capsella	4	Y	S	A	*C. rubella*	Y	219 Mb	4
Chamaecrista	300	Y	S	A	*C. fasciculata*	U	650 Mb	4+
Clarkia	40	Y	S	A	*C. xantiana*	U	750 Mb	4+
Dalechampia	130	Y	S	M	*D. scandens*	N	Unknown	Unknown
Helianthus	49	Y	S	A	*H. annuus*	Y	~3.5 Gb	6
Impatiens	1000+	Y	S	A	*I. capensis*	N	~1.5 Gb	12
Ipomoea	600+	Y	S	A	*I. purpurea*	Y	~814 Mb	2-3
Ipomopsis	9	Y	S	A	*I. aggregata*	N	~4 Gb	~7 years in the field
Medicago	87	Y	S	A	*M. truncatula*	Y	465 Mb	3
Mimulus	100+	in progress	S	A	*M. guttatus*	Y	430 Mb	2
Panicum	400+	Y	X, *P. maximum*	A	*P. virgatum* and *P. hallii*	Y	1.1 Gb (*P. virgatum*) and 550 Mb (*P. hallii*)	12 (*P. virgatum*) and 1.5-2 (*P. hallii*)
Raphanus	4+	Y	S	A	*R. raphanistrum*	Y	402 Mb (*R. sativus*) and 515 Mb (*R. raphanistrum*)	Unknown
Schiedea	32	Y	S	W	*S. globosa*	N	~1.6 Gb	Unknown
Silene	800+	Y	S	S	*S. latifolia*	Y	2.8 Gb	~9
Solanum	1200+	Y (Lycopersicon group)	S	A	*S. lycopersicum*	Y	~900 Mb	3.5+

(Continues)

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 (Continued)

Genus	Traits of primary model species						Research areas	Representative references
	QTL mapping[E]	GWAS[F]	Public accessions[G]	Life history[H]	Polyploidy[I]	Mating system[J]		
Aquilegia	Y	N	Y, OPGC	P	D	SI[4]	Flower color and development; hybridization; plant-pollinator interactions; adaptive radiations	(Kramer, 2009; Puzey and Kramer, 2009; Kramer and Hodges, 2010; Fior et al., 2013; Thairu and Brunet, 2015; Filiault et al., 2018; Jiang et al., 2020; Min and Kramer, 2020; Cabin et al., 2022)
Arabidopsis	Y	Y	Y	A	D[3]	SC	Cellular and molecular biology, development, genetics and genomics, evolution, ecology	(Atwell et al., 2010; Fournier-Level et al., 2011; Wilczek et al., 2014; Alonso-Blanco et al., 2016; Exposito-Alonso et al., 2019; Kinoshita and Richter, 2020; Fournier-Level et al., 2022; Monroe et al., 2022)
Boechera	Y	Y	Y, ABRC	P	D/P	SC	Evolution and ecology of apomixis, biotic interactions and herbivory, chemical defense, microbial ecology, flowering time, climate change	See main text
Brassica	Y	Y	Y, USDA	A[1]	D[3]	SI	Domestication, evolution of polyploidy, synthetic polyploidy, resurrection studies, biological responses to climate change	(Siemens et al., 2002; Franks et al., 2007, 2016; Franks, 2011; The Brassica rapa Genome Sequencing Project Consortium et al., 2011; Yu et al., 2013; Kitashiba and Nasrallah, 2014; O'Hara et al., 2016; Hamann et al., 2018; Qiao et al., 2020; Kaur et al., 2021; Mabry et al., 2021) (S. Turner-Hissong, Bayer, pers. comm.)
Capsella	Y	Y, *C. grandiflora*	N	A	D[3]	SC[5]	Mating system evolution, maintenance of variation, floral/leaf/fruit evolutionary development	(Guo et al., 2009; St. Onge et al., 2011; Slotte et al., 2013; Lafon-Placette et al., 2018; Sicard and Lenhard, 2018; Yang et al., 2018; Koenig et al., 2019; Niu et al., 2019; Dziasek et al., 2021) (E. Josephs, Michigan State University, pers. comm.)
Chamaecrista	N	N	Y, USDA	A	D	SC	Local adaptation, mating system evolution, evolution of nodulation, species interactions	(Fenster and Galloway, 2000a, b; Galloway and Fenster, 2000; Anon, n.d.) (S. Wadgymar, Davidson College, pers. comm.)
Clarkia	N	N	N	A	D	SC	Mating system evolution, life history evolution, speciation, ecophysiology	(Moeller, 2004; Geber and Eckhart, 2005; Eckhart et al., 2010; Pettengill and Moeller, 2012; Gould et al., 2014) (S. Sianta, University of Minnesota, pers. comm.)

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 (Continued)

Genus	Traits of primary model species: QTL mapping[E]	GWAS[F]	Public accessions[G]	Life history[H]	Polyploidy[I]	Mating system[J]	Research areas	Representative references
Dalechampia	N	N	N	P	P	SC	Evolution of floral morphology, quantitative traits, plant pollination	(Armbruster, 1993; Vanzela et al., 1997; Armbruster et al., 2009; Opedal et al., 2016)
Helianthus	Y*	Y	Y, USDA	A[1]	D[3]	SI (wild), SC (cultivated)	Speciation, adaptation, genome and chromosomal evolution, domestication, invasion/weediness, biotic interactions	(Rieseberg et al., 1998, 2003; Lexer et al., 2003; Timme et al., 2007; Kane et al., 2013) (K. Ostevik, University of California Riverside, pers. comm.)
Impatiens	N	N	N	A[1]	D	SC	Evolution of phenotypic plasticity; mating system evolution; invasion	(Hooker, 1908; McCall et al., 1994; Pyšek and Prach, 1995; Willis and Hulme, 2002; Heschel et al., 2005; Bartomeus et al., 2010; Day et al., 2012)
Ipomoea	in progress	N	Y	A[1]	D[3]	SC[5]	Mating system evolution, floral color evolution, plant/insect and plant/pathogen interactions, evolution of herbicide resistance, invasion, weediness	(Simms and Rausher, 1989; Tiffin and Rausher, 1999; Coberly and Rausher, 2003; Baucom et al., 2011; Kuester et al., 2016; Van Etten et al., 2016, 2020; Gupta et al., 2021) (R. Baucom, University of Michigan, pers. comm.)
Ipomopsis	Y	N	N	P[2]	D[3]	SC	Evolution of floral traits and plant-pollinator interactions; ecophysiology; natural selection; biological response to global change	(Campbell, 2019; Campbell et al., 2022; Navarro et al., 2022; Powers et al., 2022a) (T. Juenger, University of Texas Austin, pers. comm.)
Medicago	Y	Y	Y, stock center and mutant collections	A[1]	D[3]	SC	Functional genomics and evolution of plant-microbe symbiosis	(Küster et al., 2006; Benedito et al., 2008; Friesen et al., 2010, 2014; Stanton-Geddes et al., 2013; Yoder et al., 2014; Pecrix et al., 2018) (L. Burghardt, Pennsylvania State University, pers. comm.)
Mimulus	Y	Y	available upon request of *Mimulus* researchers	A/P	D/P	SC	Population genomics of adaptive radiations, speciation, evolution of perenniality, photoperiod evolution, mating system evolution, pollination biology, edaphic adaptation, evolution of conflict	(Hall and Willis, 2006; Lowry et al., 2008, 2019; Hall et al., 2010; Lowry and Willis, 2010; Wu et al., 2010; Brandvain et al., 2014; Kenney and Sweigart, 2016) (J. Coughlan, Yale University, pers. comm.)
Panicum	Y	Y	Y, USDA	P	P	SI	Local adaptation, biofuels, evolution of polyploidy	(Warmke, 1954; Lovell et al., 2018, 2021; Napier et al., 2022)
Raphanus	Y	Y (*R. sativus*)	Y (*R. sativus*)	A[1]	P[3]	SI	Floral evolution and plant-pollinator interactions; evolutionary ecology of invasive species; domestication	(Sampson, 1964; Stanton et al., 1989, 1991; Conner and Via, 1993; Conner et al., 2014; Moghe et al., 2014; Mun et al., 2015;

(Continues)

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 (Continued)

Genus	Traits of primary model species: QTL mapping[E]	GWAS[F]	Public accessions[G]	Life history[H]	Polyploidy[I]	Mating system[J]	Research areas	Representative references
								Yu et al., 2019; Alexandre et al., 2022; Arro and Labate, 2022)
Schiedea	N	N	N	P	D	SC	Inbreeding depression, evolution of breeding systems, adaptive radiations	(Sakai et al., 1989; Sakai and Weller, 1991; Filatov and Burke, 2004; Kapralov et al., 2009; Wallace et al., 2009; Powers et al., 2022b)
Silene	Y	N	N	P	D[3]	SC	Evolution of sexual systems and sex chromosomes; evolution/dynamics of disease; invasions	(Morris and Doak, 1998; Blair and Wolfe, 2004; Wolfe et al., 2004; Bernasconi et al., 2009; DeMarche et al., 2018) (L. Delph, Indiana University, pers. comm.)
Solanum	Y	Y	Y, stock center and mutant collections	A/P	D[3]	SC[5]	Speciation, mating system evolution, ecological adaptation, evolution of fruit, flower, and leaf morphology, plant defense, domestication	(Moyle, 2008; Schwarz et al., 2014; Szymański et al., 2020)

Notes:

[A]Phylogeny available: Y = Yes; N = No.

[B]Apomixis: S = Syngamy; X = Apomixis.

[C]Sexual traits: S = Sex chromosomes present; A = Autosomes only; M = Monoecy; W = Wind-pollinated and sub-dioecious.

[D]Annotated genome: Y = Yes; N = No; U = Unpublished.

[E]QTL mapping done: Y = Yes; N = No.

[F]GWAS (genome-wide association study) panels have been developed: Y = Yes; N = No.

[G]Public accessions are available: Y = Yes; N = No; ABRC = Arabidopsis Biological Resource Center; USDA = U.S. Department of Agriculture; OPGC = Ornamental Plants Germplasm Center.

[H]Life history: A = Annual; P = Perennial.

[I]Polyploidy: D = Diploid; P = Polyploid.

[J]Mating system: SC = Self-compatible; SI = Self-incompatible.

*QTL studies have been done based on crosses of *H. annuus* × *H. petiolaris*; many agricultural QTL studies have also been conducted.

[1]Perenniality is found in other species in the genus.

[2]Although *Ipomopsis aggregata* is a perennial semelparous species, there are annual and biennial species in the genus.

[3]There are also polyploid species in the genus.

[4]There are also self-compatible species in the genus (e.g., *Aquilegia canadensis*).

[5]There are also self-incompatible species in the genus.

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

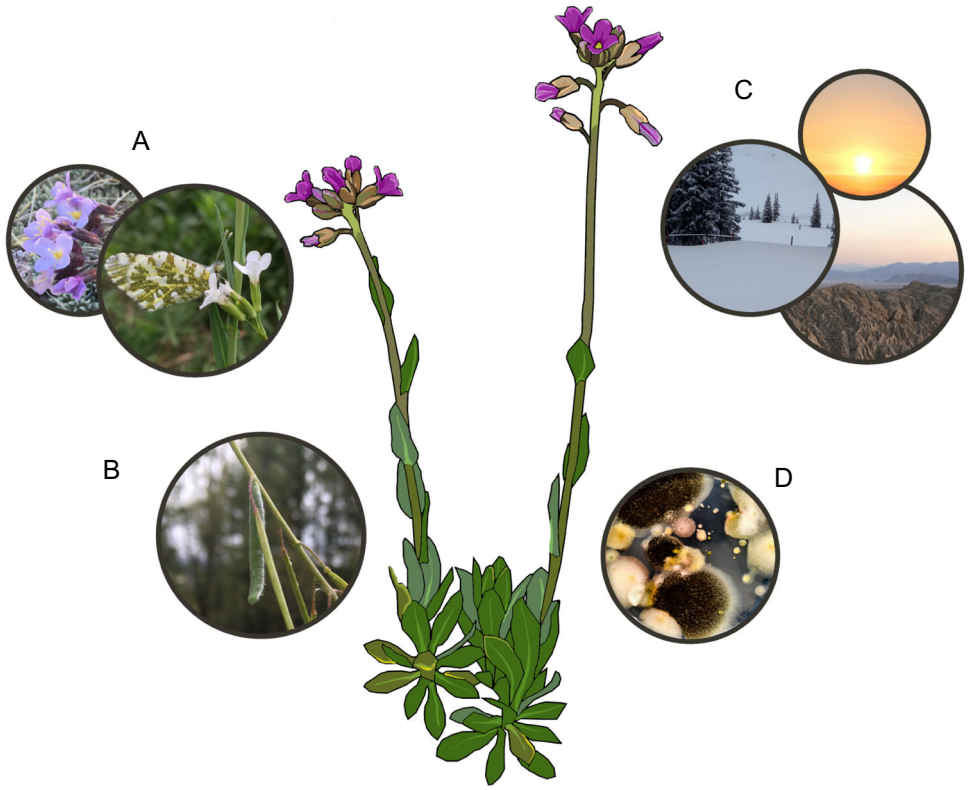

FIGURE 1 *Boechera* provides an excellent system in which to address major questions in evolutionary biology. (A) The evolution of reproductive variation. Both apomixis and self-fertilization are likely maintained by both inbreeding and outbreeding depression (Rushworth et al., 2020). (B) The role of balancing selection in evolution of complex traits. Phenotypic evolution in *Boechera* has been shaped by multiple, interacting selection pressures such as herbivory and drought (Prasad et al., 2012; Carley et al., 2021). (C) Anthropogenic climate change (Wadgymar et al., 2018a, 2018b; Anderson and Wadgymar, 2020; Hamann et al., 2021a). (D) Natural microbial variation underlies plasticity in plant traits. Microbial community affects flowering time (Wagner et al., 2014), and host genotype influences leaf microbial diversity (Wagner et al., 2016). Photos by Catherine Rushworth, Lauren Carley (A), Jill Anderson (C), and Nichole Ginnan (D).

indicated by the strong association between outcrossing and the origination of apomictic lineages (Beck et al., 2012; Rushworth et al., 2020), but very little is known about the pollinators involved.

The evolution of asexuality is a fundamental question in evolutionary biology. In addition to *Boechera*, several other genera in the mustard family reproduce apomictically, including other members of the tribe Boechereae (Mandáková et al., 2020). In plants, apomixis has evolved repeatedly and has been documented in nearly 20% of angiosperm families (Hojsgaard et al., 2014). Its widespread occurrence across the plant tree of life suggests evolutionary importance, and apomixis research has largely focused on identifying the environments in which apomixis has evolved and its genetic basis, with recent developments in grasses (Conner et al., 2015; Khanday et al., 2019) and dandelions (Underwood et al., 2022). Identifying the genes underlying apomixis will enable future implementation of apomixis as an agricultural tool (Pennisi, 2010)—for example, to perpetuate superior hybrid phenotypes or to ensure crop productivity against declines of pollinator species. While this body of research lays the foundation for understanding the evolution and ecology of apomixis, numerous questions remain. For example, how many times has apomixis evolved across the tree of life, and what genetic or ecological factors have influenced these events? Why are apomixis loci often located in highly heterochromatic genomic regions? What phenotypes underlie selection on reproductive strategies in wild populations, and how are ecologically important traits shaped by reproductive diversity?

Research in *Boechera* offers key insights into the genetics, ecology, and evolution of sex. While the co-occurrence of apomixis with polyploidy and hybridization complicates its study (Asker and Jerling, 1992), apomixis occurs at both the diploid and polyploid level in *Boechera*, and apomicts appear to be derived from outcrossing or hybridization events (Beck et al., 2012; Li et al., 2017). Aneuploidy is also well documented in apomicts (Kantama et al., 2007; Mandáková et al., 2015), akin to that in asexually reproducing cancer cells (Ben-David and Amon, 2020) and pathogenic fungi (Ni et al., 2013), leaving *Boechera* poised to become an ecological model system for the evolution and ecology of chromosomal imbalance, and its role in asexual reproduction in an agricultural context. The unique complement of traits and ecological tractability enable *Boechera* as an excellent system to address critical

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License



FIGURE 2 *Boechera* enables large-scale experiments in field and controlled conditions. Field experiments: (A) Censusing during the summer field season. (B) Replicated, randomized blocks in field site. (C) Blocks are planted into the natural vegetation. (D) An experimental plant within a block. Controlled condition experimental setup: (E) A large growth chamber experiment. (F) Close-up of a single experimental block. Photos by Lauren Carley (A and B) and Maggie Wagner (C–F).

open questions linking ecology and evolution, including: How do abiotic and biotic factors shape the origins and maintenance of apomixis in natural environments? How does apomixis alter ecologically relevant phenotypes, in turn shaping patterns of selection and population dynamics? How do apomixis and mating system interact to shape patterns of gene flow, thus impacting species formation and hybrid zone dynamics?

Classic population genetic theory predicts that an asexual lineage will proliferate upon origin due to reproductive assurance, but decline over time because of deleterious mutation accumulation and the inability to recombine beneficial mutations onto a single background, slowing adaptation to novel or changing environments (Maynard Smith, 1978). Consistent with these predictions, genomic analyses indicate that asexual *Boechera* lineages display greater mutation accumulation than sexual lineages (Lovell et al., 2017). Nevertheless, the predicted decline due to mutation load may be slowed or offset when new asexual lineages originate frequently, when asexuals are facultative (reproducing both sexually and asexually), or when the local environment, and thus selection, is temporally and/or spatially heterogeneous. Evidence in *Boechera* suggests both a single origin of apomixis that spreads via outcrossing of apomictic pollen onto different genetic backgrounds (Lovell et al., 2013, 2014) and multiple transitions to apomixis, potentially occurring with each hybridization event (Carman, 1997; Mau et al., 2015). Tracking of apomict-by-sexual crosses across multiple generations shows inheritance of apomixis in the F3 generation, confirming that apomictic pollen may spread onto sexual backgrounds (Mau et al., 2021). Whether apomixis alleles evolved once or more often, future

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

studies examining the genetic or ecological decline of asexual populations should take into account the great diversity of apomictic *Boechera* lineages (Beck et al., 2012; Mau et al., 2015; Li et al., 2017).

Detecting the loci underlying apomixis depends on robust identification of wild apomictic lineages, which is enabled by novel genotyping methods (Corral et al., 2013; Mau et al., 2013; Li et al., 2017). Over the last decade, key advances made in *Boechera* include identification of regulatory changes between asexuals and sexuals (Sharbel et al., 2010; Amiteye et al., 2011), apomixis-specific alleles in the genes *UPGRADE2* and *APOLLO* (Corral et al., 2013; Mau et al., 2013), and successful reference-free genome assembly of highly heterozygous apomictic accessions (Brukhin et al., 2019).

Absent recombination and segregation, asexual lineages and populations may lack ability to adapt to changing environments (Maynard Smith, 1978). Habitat preferences and species distributions could differ between asexual and sexual organisms (geographical parthenogenesis; Hörandl, 2006; Whitton et al., 2008). Nevertheless, one large-scale study showed no evidence of geographic parthenogenesis in *Boechera*, with asexuals occupying their parental niches (Mau et al., 2015). Within smaller geographic regions, niches differ between sexuals and asexuals and between asexual groups representing different parental combinations, suggesting that hybridization shapes environmental preference (Rushworth et al., 2018).

Ecology influences the evolution and maintenance of apomixis in nature. Across five common garden sites, overwinter survival of apomictic *Boechera* lineages was consistently higher than sexual survival; however, asexual lineages experienced substantially higher insect herbivory during the reproductive season, which in turn reduced survival in subsequent years (Rushworth et al., 2020). Thus, both the abiotic and biotic environment influence the evolution of sex, consistent with observations in sexual and asexual freshwater snails (Lively and Morran, 2014). The use of diploid accessions in this study (Rushworth et al., 2020) revealed the fitness effects of apomixis independent of polyploidy. Additionally, apomicts derived from both intraspecific and interspecific outcrossing events had high survival, consistent with heterosis; in contrast, herbivory was highest on interspecific asexuals, suggesting outbreeding depression in some defense traits. Tradeoffs between early growth and chemical defenses offer a promising avenue for future studies. Further work should also characterize the complex genomic landscape of inbreeding and outbreeding depression, identify the molecular changes that underlie these fitness shifts, and disentangle the relationship between hybridization and apomixis.

Boechera diversity

Rapid divergence and rampant hybridization create complex relationships among the roughly 80 sexual *Boechera* species (Li et al., 2017). Similar to other rapid radiations with incomplete reproductive isolation, *Boechera* provide unique opportunities for understanding speciation dynamics. However, a resolved genus-wide phylogeny is not yet available and may be complicated by the existence of hybrids, which violate the assumptions of most phylogenetic methods. Phylogenetic analysis of 58 sexual species successfully identified subclades within *Boechera*, but relationships among these clades remain unresolved (Alexander et al., 2013). Recent studies have clarified relationships within several different clades, including the *Boechera fendleri* group (Alexander et al., 2015b), the *Boechera suffrutescens* group (Morin et al., 2018), and the *Boechera puberula* group (Schilling et al., 2018). Similar issues—backbone discordance and hybridization—have complicated phylogenetic resolution of other, similarly diverse ecological model systems such as *Mimulus* (Beardsley et al., 2004; Morales-Briones et al., 2022) and *Aquilegia* (Fior et al., 2013) Two additional issues lend further complexity to phylogenetic resolution of *Boechera*: (1) the prevalence of polyploids (Schranz et al., 2005) and (2) the possibility of de novo evolution of sexual populations from rare recombination in facultatively asexual lineages (Carman et al., 2019), which would result in novel hybrid species like those found in other plant groups (e.g., Rieseberg et al., 2003). Newer methods have enabled robust resolution of Brassicaceae more broadly (Nikolov et al., 2019). Novel reduced-representation (Jordon-Thaden et al., 2020) and phylogenetic methods (De Maio et al., 2015; Hendriks et al., 2021) offer promise for a robust phylogeny of *Boechera*, which is currently in progress (M. D. Windham, Duke University, personal communication).

Despite its phylogenetic complexity, cytological work has improved our understanding of evolution in this group. Using comparative chromosomal painting (CCP), Mandáková et al. (2020) identified an ancestral cruciferous karyotype of $x = 8$ in the sister tribe Halimoboleae and the causes of chromosome loss in Boechereae (which has a base number of $x = 7$). Chromosomal inversions and translocations are shared among multiple species within the Boechereae (Mandáková et al., 2020) and offer promise to resolve conflicts between the existing *Boechera* phylogeny (Alexander et al., 2013) and a larger Brassicaceae phylogeny (Beilstein et al., 2010). For example, while Alexander et al. (2013) found weak evidence for a clade including *B. oxylobula* and *B. gracilipes*, to the exclusion of *B. formosa*, a 9.83-Mb inversion shared by *B. formosa* and *B. oxylobula* suggests they are sister species. In contrast, conflicts remain between outgroup *Nevada* and Boechereae genera *Phoenicaulis* and *Borodinia*, where both putative sister taxa share one inversion with *Nevada* (Mandáková et al., 2020). Extensive chromosomal divergence suggests a role for inversions and translocations in *Boechera* speciation, as seen in *B. stricta* ecotypes, which are polymorphic for an inversion on Chromosome 1 (Lee et al., 2017).

Extensive diversity within *Boechera* offers many possibilities for studies of hybridization and speciation. Diploid hybridization is common in *Boechera* habitats (Alexander et al., 2013; Carman et al., 2019), and hybrids or controlled

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

crosses can generate interspecific pedigrees (Mau et al., 2021; Rushworth and Mitchell-Olds, 2021) for trait mapping or transcriptomics (Hibbins and Hahn, 2021). Patterns of speciation in *Boechera* are likely complex due to substantial shared variation and hybridization among taxa. Artificial crosses between *B. retrofracta* and *B. stricta* reveal prezygotic and postzygotic reproductive isolation including unilateral asymmetry in crossing success, such that interspecific crosses succeed only when *B. stricta* is the maternal parent (Rushworth and Mitchell-Olds, 2021). Future work will characterize reproductive isolation in this complex group and assess the relative importance of mating system variation, genetic load, and hybrid incompatibilities in hybrid zone dynamics.

Variation in *Boechera stricta*

Boechera stricta is widespread across western North America and has been the focus of many eco-evolutionary studies. Populations from the Rocky Mountains and intermountain west comprise two subspecies (Lee and Mitchell-Olds, 2011, 2013). The western subspecies typically occupies habitats with greater water availability than the eastern subspecies (Lee and Mitchell-Olds, 2013). Furthermore, the subspecies differ for a major QTL that influences morphology and fecundity (Lin et al., 2021). In addition, a number of genomic regions associated with precipitation show genetic divergence between subspecies. Analysis of whole-genome resequencing data from >500 *B. stricta* accessions validated the western subspecies and identified three genetic groups (COL, UTA, and NOR) within the eastern subspecies (Wang et al., 2019). Geographic overlap among groups is modest, except for sympatry in parts of Montana and Idaho between the western subspecies and the NOR group of the eastern subspecies. Coalescent simulations suggest eastern and western subspecies separated about 180 kya, and the subgroups of the eastern subspecies diverged about 30–70 kya. Historical effective population sizes range from 10^4–10^5, with low levels of gene flow among population groups (Wang et al., 2019). Future research in areas where the species is uncommon (California, Nevada, the Pacific Northwest, Canada, and Alaska) will enhance our understanding of population differentiation and adaptation of *B. stricta* across its entire range.

About 10% of the *B. stricta* genome shows elevated polymorphism compatible with long-term balancing selection, but not with variation in mutation rate, recombination rate, or gene density (Wang et al., 2019). These regions show a 6-fold enrichment of NBS-LRR genes, suggesting balancing selection on disease resistance genes (Karasov et al., 2014; Koenig et al., 2019). Furthermore, these balanced regions in *B. stricta* are syntenic with regions of elevated polymorphism in *A. thaliana* (Clark et al., 2007), suggesting long-term balancing selection since the divergence of these genera (Wang et al., 2019). Likewise, in a large study of five *Primulina* (Gesneriaceae) species, Ke et al. (2021) found that ancient polymorphism in some genomic regions contributed to adaptation and speciation of endemic species. Thus, differential sorting of old polymorphisms can influence divergent genomic regions among populations or congeners.

Genetic architecture of complex traits

Information on population structure enables GWAS identification of candidate genes controlling the ecology and evolution of functional traits. Although this task has rarely been accomplished for native plants in their natural habitats, GWAS hits can have resolution within a handful of genes (Brachi et al., 2010; Monnahan et al., 2021; Yan et al., 2021). Using this approach, Yan et al. (2021) analyzed flowering time variation for ~400 genotypes across 10 environments in *B. stricta*. They found two large effect flowering QTLs and dozens of significant QTLs that control flowering time, association with the climate in home environments, or genotype × environment interactions. Closely linked candidate genes near QTL peaks suggest that regulatory genes contribute to genotype-by-environment interaction affecting complex traits.

One variant (*qtl6.2*, near the *TERMINAL FLOWER 1* candidate gene; Wickland and Hanzawa, 2015) controls up to 14.6% of the genetic variation in flowering time. The derived allele at this locus delays flowering and is more common in sites with greater water availability. As expected for a widespread species growing across heterogeneous environments, molecular population genetic searches for adaptive nucleotide variation found little evidence for hard selective sweeps that favored new variant alleles (Stephan, 2019). Instead, at least one large-effect QTL showed significant evidence for a soft selective sweep on standing variation. Thus, nucleotide polymorphism data from the *B. stricta* GWAS panel can identify ecologically important QTLs and reveal historical selection on candidate genes using molecular population genetics.

Finally, the experimental tractability of *Boechera* has enabled progress toward understanding the role of pleiotropy in functional trait evolution. Pleiotropy occurs when a genetic polymorphism influences variation in several traits or development of a single trait in several environments (Auge et al., 2019). To understand the evolutionary significance of pleiotropy, high-resolution GWAS analyses can examine data from multiple traits, environments, or studies (Watanabe et al., 2019; Yan et al., 2021). Antagonistic selection on pleiotropic traits may constrain responses to natural selection (Auge et al., 2019; Keith and Mitchell-Olds, 2019; Tsuchimatsu et al., 2020). Genome-wide association studies showing that alternate QTL alleles are favored in specific environments suggest antagonistic pleiotropy for climate-related traits (Hamilton et al., 2015; Yan et al., 2021). Genome-wide association studies in *Boechera* and *Arabidopsis* will

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

facilitate further evolutionary analysis of pleiotropic constraints.

Selection and local adaptation

Environmental conditions vary spatially and temporally across the landscape, especially in mountainous systems where the environment can change substantially over short distances (Körner, 2007), potentially driving local adaptation at small spatial scales (Hereford, 2009). Like many systems, *Boechera* exhibits substantial trait variation and genetic differentiation across populations (Song and Mitchell-Olds, 2007; Lee and Mitchell-Olds, 2011, 2013; Leamy et al., 2014; Anderson and Gezon, 2015; Wadgymar et al., 2017). Field, greenhouse, and growth chamber experiments in *B. stricta* have demonstrated strong local adaptation, across eastern and western subspecies (Lee and Mitchell-Olds, 2011, 2013) and within regions (Anderson et al., 2015; Anderson and Wadgymar, 2020).

A fundamental question in evolutionary ecology is whether genetic polymorphisms are contextually beneficial and maintained by balancing selection (Delph and Kelly, 2014; Charlesworth, 2015) or are deleterious but not yet been eliminated by selection (Huang et al., 2016). Field experiments with *B. stricta* recombinant inbred lines transplanted into parental environments in Colorado and Montana revealed that local adaptation arises through both genetic trade-offs and conditional neutrality at fitness-related QTL (Anderson et al., 2013, 2014). For example, at a key flowering phenology QTL, the local allele conferred a fitness advantage in its home site and incurred a fitness cost in the alternative environment (Anderson et al., 2013). However, in other portions of the genome, the local allele is advantageous in its home environment but has no fitness cost elsewhere (conditional neutrality, Anderson et al., 2013).

One key result to emerge from studies of *B. stricta* is the importance of water availability in driving local adaptation. Lee and Mitchell-Olds (2011) genotyped accessions from 239 natural populations across western North America and discovered that the primary drivers of population divergence included winter precipitation and distance to the nearest stream. Subsequent greenhouse experiments documented that trait divergence aligns with the niche models, such that water availability—and other selective pressures—likely underlie local adaptation (Lee and Mitchell-Olds, 2013). A separate greenhouse manipulation of water and nutrient availability found that fitness declined with source elevation for Colorado accessions exposed to drought stress (MacTavish and Anderson, 2020), which is consistent with local adaptation of low-elevation accessions to restricted water availability (Anderson and Wadgymar, 2020). Finally, a field study in five Colorado gardens revealed local adaptation to historical winter snowpack, again highlighting the importance of water in exerting selection on natural populations (Anderson and Wadgymar, 2020). Taken together, these results suggest that balancing selection operates across the landscape to maintain quantitative genetic variation.

Common garden experiments in Colorado uncovered clear concordance between optimal trait values for specific leaf area from multivariate genotypic selection analyses and the values expressed by local accessions (Wadgymar et al., 2017). These results confirm that natural populations have adapted to their local selective regime and that genetically based clines likely evolved in response to variable selection across elevations. However, local trait values did not correspond with the optima for flowering phenology. Instead, selection favored earlier flowering at larger sizes, with local accessions lagging behind optimal flowering times by >10 days in both gardens and reproducing at 5–10 cm shorter stature than optimal (Wadgymar et al., 2017). This maladaptive trait expression of local genotypes could arise if climate change has shifted the adaptive landscape, as other studies in this system have documented that novel climates favor accelerated reproduction (Anderson et al., 2012; Bemmels and Anderson, 2019). Alternatively, selection on linked traits could constrain the evolution of flowering time.

Genetic correlations between complex traits can constrain adaptive responses to selection (Etterson and Shaw, 2001). Studies in *B. stricta* have evaluated these constraints primarily by modeling the genetic variance–covariance (**G**) matrix (Anderson et al., 2012; Bemmels and Anderson, 2019; Hamann et al., 2021b; Keith and Mitchell-Olds, 2019; MacTavish and Anderson, 2020, 2022). A reciprocal transplant experiment in Colorado of *B. stricta* accessions into ambient conditions and early snow removal (simulating climate change) found that limited genetic variation in complex traits will present a larger impediment to adaptation to novel conditions than genetic correlations across traits (Bemmels and Anderson, 2019). However, a common garden experiment in Idaho revealed strong genetic correlations between the profile of secondary defenses (glucosinolates) in leaf and fruit tissues, which was antagonistic to the direction of selection (Keith and Mitchell-Olds, 2019). Thus, genetic correlations can restrict evolutionary responses to selection in *B. stricta*. Together, these studies indicate that the extent to which genetic covariances constrain or facilitate adaptive responses to selection likely depends on the traits that are the most important for local adaptation.

Glucosinolates and ecological variation

Glucosinolates are secondary metabolites in the Brassicaceae that influence biological interactions with mammalian and insect herbivores (Hopkins et al., 2009) and pathogens and microbial mutualists (Halkier and Gershenzon, 2006; Bressan et al., 2009; Poveda et al., 2020). Biochemical and evolutionary genetics of glucosinolates have been studied extensively in *Arabidopsis* (Brachi et al., 2015; Davila Olivas et al., 2017; Katz et al., 2021). In *B. stricta*, ecologically important glucosinolate variation includes polymorphism for the proportion of aliphatic glucosinolates derived from

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

branched-chain amino acids ("BC-ratio"). This variation is controlled by a tandem duplication of a *Branched-Chain Methionine Allocation* (*BCMA*) locus, with selectively favored amino acid changes causing a gain of enzyme function, enabling synthesis of glucosinolates derived from branched-chain amino acids (Prasad et al., 2012). This cytochrome P450 locus controls metabolic flux in the *Arabidopsis thaliana* glucosinolate pathway (Olson-Manning et al., 2013), with higher flux causing lower feeding rate by a generalist insect herbivore (Olson-Manning et al., 2015). The *BCMA* QTL has small effects on herbivore damage in nature (Carley et al., 2021). Across 16 environments in Idaho and Colorado, *BCMA* alleles show significant rank changes in herbivore damage and survival, suggesting that this polymorphism is maintained by balancing selection (Carley et al., 2021). The rank changes in herbivore damage between the *BCMA* alleles may reflect differences in herbivore communities or abundances among sites and years (Figure 3), although this hypothesis remains to be tested.

Glucosinolates also affect drought tolerance in *Arabidopsis* and *B. stricta* (Hossain et al., 2013; Salehin et al., 2019; Carley et al., 2021). Notably, the *BCMA* allele for methionine-derived glucosinolates enables plants to reduce their water-use under drought stress, thereby augmenting fitness during droughts (Carley et al., 2021). The exact mechanisms linking glucosinolate variation to drought tolerance in *B. stricta* have not yet been identified. However, more is known in *Arabidopsis*, where several glucosinolate-derived compounds regulate stomatal closure by inducing buildup of reactive oxygen species in guard cells (Hossain et al., 2013; Salehin et al., 2019). Spatial variation across the landscape favors different alleles of the *BCMA* gene, likely due to heterogeneity in water availability and rates of herbivory (Carley et al., 2021). In Colorado, high-elevation *B. stricta* populations experience less herbivory than low-elevation populations (Anderson et al., 2015), and aridity decreases with elevation (Anderson and Wadgymar, 2020). When accessions originating from a range of elevations are planted in common gardens, resistance to insect herbivory declines with source elevation across years and sites (Anderson et al., 2015), which we hypothesize is an evolved response to reduced herbivore pressure at high elevation. Thus, in this region, the rate of herbivory covaries with drought stress, and pleiotropy at the *BCMA* locus could influence fitness of low-elevation genotypes in future climates, if both drought stress and herbivore pressures increase (Hamann et al., 2021b; Masson-Delmotte et al., 2021).

Phenotypic plasticity

Most plant species studied to date express phenotypic plasticity in one or more traits (Palacio-López et al., 2015). Adaptive plasticity can evolve when individuals confront multiple environments within their lifespans and they can accurately sense and respond to predictable shifts in environmental conditions, genetic variation exists for

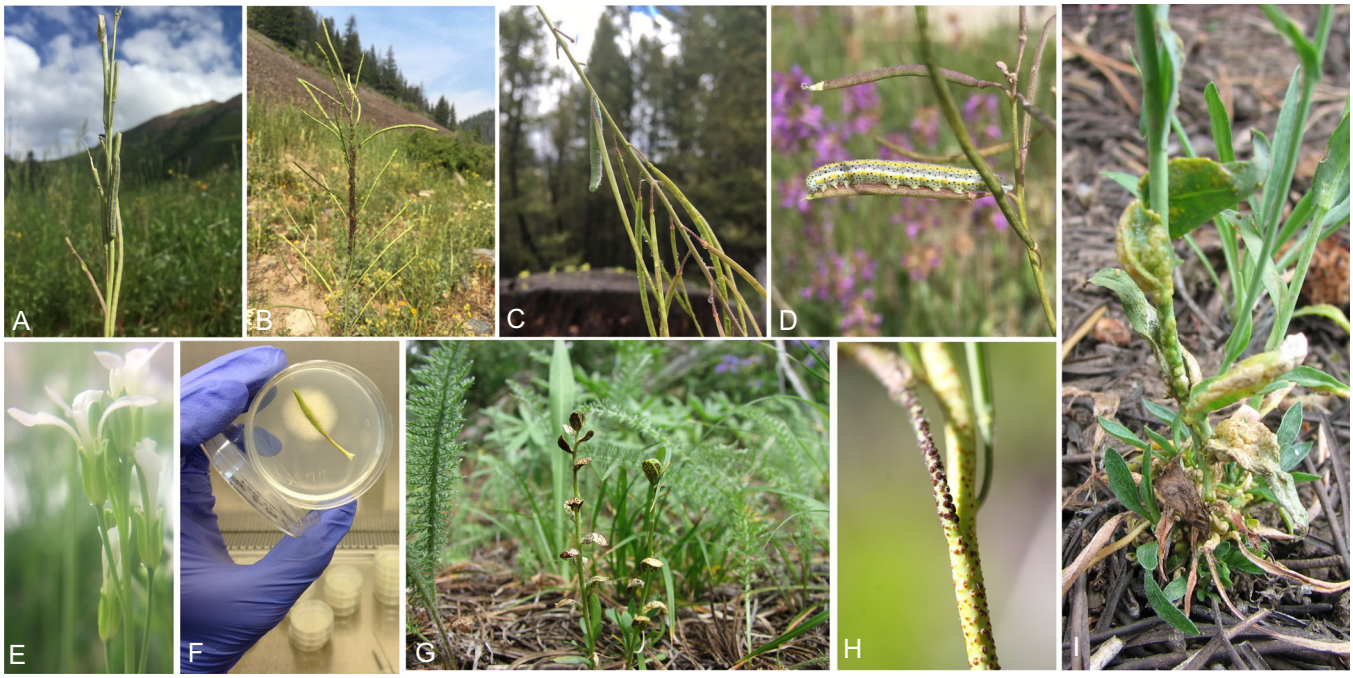

FIGURE 3 *Boechera* interacts with diverse natural enemies and potentially beneficial symbionts. (A–D) Common insect herbivores on *Boechera*. (A) *Euchloe* sp. caterpillar on wild *Boechera stricta*. (B) Aphids on wild *Boechera stricta* hybrid. (C) *Anthocharis sara* caterpillar and (D) *Pontia* sp. caterpillar on wild *B. retrofracta* hybrids in Idaho. (E) Droplets of extrafloral nectar at the base of *B. stricta* sepals. (F) Fungal endophyte emerging from a healthy, surface-sterilized *B. stricta* leaf. (G) *Puccinia* rust fungus infecting *B. stricta* in Idaho. (H) *B. stricta* stem infected by *Leptosphaeria*. (I) An unidentified gall-forming pathogen (perhaps *Synchytrium*) disfiguring the lower stem and cauline leaves of *B. stricta* in central Idaho. Photos by Lauren Carley (A, B), Catherine Rushworth (C, D), Maggie Wagner (E), Posy Busby (F, G, I), and Thomas Mitchell-Olds (H).

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

plasticity, and gene flow is extensive relative to the spatial scale of environmental variation, such that the progeny establish in environments different from those of their parents (Levins, 1963; Moran, 1992; Alpert and Simms, 2002; Sultan and Spencer, 2002; Reed et al., 2010; Hendry, 2015; Palacio-López et al., 2015). In montane ecosystems, the environment differs dramatically over short spatial scales across elevations (e.g., Körner, 2007). Thus, alpine plants–even those with short-distance movement of seed and pollen—could routinely disperse their offspring into nonparental conditions. Plasticity could be especially adaptive for perennial species in topographically complex landscapes because they experience fine-grained temporal and spatial variation in conditions.

Indeed, *B. stricta* maintains significant plasticity in phenological, physiological, floral, and defensive traits (Anderson et al., 2010, 2012; Anderson and Gezon, 2015; Vaidya et al., 2018; Wagner and Mitchell-Olds, 2018; Wadgymar et al., 2018a). For example, relative to low elevation, high-elevation environments induce greater stomatal density, leaf water content, specific leaf area, foliar N content, and reduced stomatal length (Anderson and Gezon, 2015). Identifying the drivers of plasticity requires manipulative studies of abiotic and biotic conditions. For instance, field and greenhouse manipulations revealed that arid, low-elevation environments and drought stress can induce pink or purple floral color in this predominantly white-flowered self-pollinating species (Vaidya et al., 2018), Similarly, variation in soil properties can induce strong shifts in flowering time (Wagner et al. 2014). These examples indicate that unexpected abiotic factors can drive the expression of floral traits typically presumed to evolve via pollinator-mediated selection. Notably, *B. stricta* harbors genetic variation for the magnitude and sometimes the direction of plasticity for a wide range of traits, including flowering time (Wagner et al. 2014), flower color (Vaidya et al. 2018), foliar glucosinolate content (Wagner and Mitchell-Olds, 2018), specific leaf area, and height at flowering (Anderson and Gezon, 2015). In fact, most traits that have been quantified under multiple conditions in common garden studies with *B. stricta* display clear evidence for genotype-by-environment interactions, indicating extensive genetic variation in the degree of plasticity in this species (Anderson et al., 2010, 2012; Anderson and Gezon, 2015; Vaidya et al., 2018; Wagner and Mitchell-Olds, 2018; Wadgymar et al., 2018a).

Plasticity does not necessarily always increase fitness. In some cases, it could be neutral or even a maladaptive stress response. Determining whether plasticity is adaptive requires selection analyses that test whether plasticity augments fitness under natural field conditions (e.g., Scheiner and Callahan, 1999; Schmitt et al., 1999). Wagner and Mitchell-Olds (2018) examined the fitness effects of plasticity in glucosinolate content of 25 *B. stricta* genotypes in four common gardens in Idaho. Overall, 73% of all genotype-specific plastic responses (i.e., the observed garden-specific genotypic values of each trait minus the experiment-wide mean genotypic value) were not strong enough to affect fitness, based on the estimated selection gradients on the same traits in the same environments. Nevertheless, when non-neutral plasticity was observed, it was advantageous more often than predicted by chance alone. Similarly, in a separate experiment in two Colorado common gardens, the direction of plasticity in functional traits was concordant with genetic clines in these traits and selection on these traits (Wadgymar et al., 2017). For example, the dry low-elevation garden induced higher water-use efficiency (plasticity), genotypes from low elevations expressed greater water-use efficiency (genetic cline), and selection via viability and fecundity favored water-use efficiency values of local genotypes (Wadgymar et al., 2017). The co-gradient nature of plasticity, genetic clines, and selection suggests that plasticity and genetic clines could have evolved in response to variable selection across the landscape. Plastic changes in ecologically important traits could facilitate adaptation to heterogeneous environments.

In addition to plasticity that is expressed within a generation, plasticity can also arise across generations, when the environment of the parents influences offspring phenotypes. Transgenerational plasticity can be advantageous if the environment is predictable, such that the conditions that parents confront are strong indicators of the conditions that offspring will experience. Researchers—including us (e.g., Anderson et al., 2010; Anderson and Wadgymar, 2020; Rushworth et al., 2020; Carley et al., 2021; Yan et al., 2021)—often treat transgenerational plasticity as a nuisance factor in eco-evolutionary studies by growing seeds under controlled conditions for ≥1 generation to homogenize maternal effects. Nevertheless, transgenerational plasticity can have important fitness consequences (Galloway and Etterson, 2007). In *B. stricta*, transgenerational plasticity influences seedling establishment and maternal effects can persist beyond the seedling stage (Wadgymar et al., 2018a). Future studies will evaluate the extent to which different aspects of the parental environment influence offspring trait expression and fitness and illuminate the role of transgenerational plasticity in mediating the effects of climate change.

Phenotypic plasticity is a trait subject to selection that can evolve as long as sufficient heritability exists (genotype-by-environment variation). Research in *B. stricta* has chronicled extensive genetic variation for plasticity in functional traits. We hypothesize that accessions from regions with greater spatial or temporal variation in conditions could maintain higher plasticity. However, glucosinolate plasticity in response to fine-grained environmental variation had no discernable fitness effects (Wagner and Mitchell-Olds, 2018). Studies that quantify genetically based clines in plasticity and evaluate whether selection on plasticity differs across the landscape will generate novel insights into the conditions under which plasticity could be adaptive. For example, in *B. stricta*, within-generation plasticity in germination success increases with source elevation in common gardens in Colorado, whereas

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

transgenerational plasticity in this trait shows the opposite pattern (Wadgymar et al., 2018a). From these patterns, we might infer that high-elevation locales have greater temporal variation in conditions relative to lower-elevation sites. This inference derives from theoretical expectations that within generation plasticity is an evolutionary response to reliable, predictable, and detectable shifts in environmental conditions that occur within the lifespan of an individual (Moran, 1992; Stratton and Bennington, 1998). In contrast, transgenerational plasticity can be favored in stable environments in which the conditions that the parents experience are tightly correlated and predictive of the conditions in which offspring will establish (Schlichting and Levin, 1986; Scheiner, 1993; Donohue and Schmitt, 1998; Galloway, 2005; Uller, 2008). Future research could examine the extent of temporal variation in climate across this elevational gradient and test whether within-generation and transgenerational plasticity differ in their fitness effects.

Microbiome

As evidence mounts that microbiomes shape their hosts' phenotype and fitness, research interest in the evolution of plant–microbiome interactions has also grown. The experimental tractability of *Boechera* makes it a prime system for investigating related topics such as the extent to which microbiome composition and function can be considered heritable "extended phenotypes" of macroorganisms; how microbiomes affect the evolutionary trajectories of plants; and the concordance or tension between the evolutionary interests of plants and microbes (O'Brien et al., 2021).

Although *Boechera* is nonmycorrhizal, the diverse communities of bacteria, fungi, and other microbes that colonize its aboveground and belowground organs are broadly comparable to those observed in mycorrhizal plants (e.g., Hestrin et al., 2021). *Boechera*-colonizing microbes appear to originate from local soil microbiomes, which—much like soil texture and chemistry—differ substantially among habitats. This naturally occurring soil microbiome variation affects flowering time and alters selection on flowering time, whereas abiotic soil variation influences phenology but not selection (Wagner et al., 2014). The effects of the microbiome on disease resistance, drought tolerance, and other functional traits have been described in other plants (Petipas et al. 2020) but remain to be explored in *Boechera*.

The existence of microbiome heritability suggests the potential for *Boechera*–microbiome interactions to have been shaped by natural selection. In a long-term, multi-site field experiment, genetic variation among five *B. stricta* populations influenced bacterial alpha- and beta-diversity in leaves, but not roots (Wagner et al., 2016). The strength of these host-genotype effects varied substantially among habitats. The causal genes and traits underlying host-genotype microbiome control in *Boechera* are currently unknown; however, ongoing work (L. Carley et al., unpublished manuscript) leverages genetic resources in *B. stricta* to test how glucosinolate variation affects rhizosphere microbiomes (Bressan et al., 2009), and how this trait-mediated community filtering influences fitness. Future research will integrate microbiome heritability into the context of *B. stricta* ecological genomics and local adaptation.

The functional roles of most *Boechera*-associated microbes are unknown, but likely diverse. For instance, ammonia-oxidizing Nitrososphaera and diazotrophic *Bradyrhizobia* colonize *B. stricta* roots (Wagner et al., 2016), potentially influencing nutrient availability. Some groups (e.g., *Burkholderia* spp.; Eberal and Vandamme, 2016) likely include both beneficial symbionts and weak pathogens. Several major pathogens of *Boechera* occur on stems and leaves, but are generally not well-characterized (Figure 3). One exception is the rust fungus *Puccinia monoica*, which causes infected plants to produce tightly packed, bright yellow, spore-laden, fragranced leaf rosettes called pseudoflowers (Rushworth et al., 2011). Pseudoflower formation results from transcriptional modification of cell differentiation, volatile synthesis, and shoot development (Cano et al., 2013). The over-representation of NBS-LRR genes in *B. stricta* genomic regions under balancing selection (Wang et al., 2019) suggests that the influence of pathogens on *Boechera* evolution may be stronger than currently appreciated.

Boechera offers the opportunity to examine temporal microbiome dynamics in perennials, which are understudied relative to annual plants. Perennial microbiomes present an interesting evolutionary scenario, where a microbial lineage originates from soil but then persists and evolves *in planta* for many generations. Carefully designed experiments can disentangle the effects of host age from seasonal weather patterns. As *B. stricta* individuals aged from 2 to 4 years, root bacterial community composition shifted, and alpha-diversity declined monotonically (Wagner et al., 2016). In contrast, host age did not influence leaf-associated microbiomes, perhaps because leaves often senesce before winter and grow anew the following spring; i.e., leaves are not necessarily perennial structures, unlike root systems which persist for years.

Global climate change

Anthropogenic climate change has influenced plant traits, fitness, and population persistence directly through elevated CO_2 concentrations, increasing temperatures, new precipitation patterns and other abiotic change (Becklin et al., 2016; Hamann et al., 2018; Walker and Ward, 2018), and indirectly through novel biotic interactions (Robinson et al., 2012; Alexander et al., 2015a; Descombes et al., 2020; Hamann et al., 2021a). *Boechera* species inhabit a dynamic landscape where the climate is changing rapidly. In particular, warming winters have reduced snowfall in high elevation and high latitude ecosystems, which has decreased the snowbank and caused snow to melt earlier in the spring

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(Mountain Research Initiative, 2015; Fyfe et al., 2017; Masson-Delmotte et al., 2021). Early snowmelt depresses plant fecundity by exposing sensitive floral tissues to frost damage, which they would not have experienced historically (Inouye, 2008). In addition, worsening winter droughts in concert with elevated spring and summer temperatures have augmented aridity, with increasingly severe consequences for the persistence of populations—especially those in the trailing range edges at lower elevations (Anderson and Wadgymar, 2020).

Boechera offers numerous opportunities to examine how shifting abiotic conditions and biotic communities influence adaptive dynamics and the risk of population decline under climate change. For one, wide-ranging species in this genus, like *B. stricta*, occur across broad latitudinal and elevational gradients, so accessions can be sourced from populations that have experienced disparate climate conditions throughout their evolution. Phylogeographic data suggest that *B. stricta* likely recolonized high-elevation and high-latitude sites rapidly after the retreat of the Pleistocene glaciers (Song et al., 2006; Kiefer et al., 2009), suggesting that this species quickly responded to episodes of climate change in the geological past. Furthermore, manipulative experiments in the field, greenhouse, and growth chamber can expose diverse accessions to historical, contemporary, and future climatic conditions (Wadgymar et al., 2018a, 2018; Bemmels and Anderson, 2019; Anderson and Wadgymar, 2020; MacTavish and Anderson, 2020). These studies evaluate how climate change could alter the adaptive landscape and whether populations could keep pace with novel conditions via plasticity or adaptation.

Plasticity could enable populations to persist through rapid anthropogenic climate change, at least in the short term (e.g., Nicotra et al., 2010; Valladares et al., 2014; De Kort et al., 2020). Climate change has advanced the flowering time of *B. stricta* by >2 weeks since the mid-1970s (Wadgymar et al., 2018b), and elevated temperatures, reduced winter duration, and early snowmelt induce early flowering (Anderson et al., 2010, 2012; Anderson and Gezon, 2015). Continued projected changes in these climatic factors (Masson-Delmotte et al., 2021) could further alter phenology in *B. stricta* and other species (Colautti et al., 2017; Wadgymar et al., 2018b). Experimental snow removal in Colorado decreases snowpack, advances snowmelt, and can reduce soil water availability, all of which are predicted to shift with climate change; additionally, snow removal induces similar advancements in flowering time as seen in long-term records (Anderson and Gezon, 2015). Ongoing selection analyses evaluate whether phenological plasticity is sufficient to maintain positive population growth rates.

Climate change has likely strongly altered patterns of natural selection, favoring traits associated with increased thermal and drought tolerance (Hamann et al., 2018) along with increased defenses against antagonists like herbivores (Hamann et al., 2021a). Self-pollinating species like *B. stricta* are likely constrained by limited within-population genetic variation even when selection strongly favors new phenotypic optima (Bemmels and Anderson, 2019). However, genetically based clines in functional traits and phenology across elevational gradients (Anderson and Gezon, 2015; Wadgymar et al., 2017) indicate that extensive among-population variation in these traits exists over short geographic scales; thus, gene flow could potentially facilitate local population persistence if genotypes from other locations express trait values closer to new optima. Novel climates have reduced fitness of local accessions (Wadgymar et al., 2018b), favoring lower elevation genotypes, which evolved in relatively hot arid climates, over local genotypes (Anderson and Wadgymar, 2020). Snow removal exacerbated this pattern, but a signature of local maladaptation emerged even under contemporary climates (Anderson and Wadgymar, 2020). Snow additions—reflecting climates of the recent past—restored the fitness advantage of local genotypes, indicating that climate change has already disrupted long-standing patterns of local adaptation in *B. stricta* (Anderson and Wadgymar, 2020). Future work examining *Boechera* trait expression and fitness under extreme events will generate more robust predictions of population persistence in a more temporally variable climate.

Herbivores exert strong selection on plants, including *Boechera* (e.g., Prasad et al., 2012; Carley et al., 2021) (Figure 3), and the extent of herbivory also varies across elevational gradients (e.g., Rasmann et al., 2014; Descombes et al., 2020). In *B. stricta*, high-elevation accessions experience greater rates of foliar damage from insect herbivores than their low elevation counterparts irrespective of the elevation of the common garden (Anderson et al., 2015); these genetic clines in herbivore resistance could reflect an evolutionary response to reduced herbivore pressure in high elevation locales. If—as predicted—rates of herbivory increase under climate change (Stiling and Cornelissen, 2007; Robinson et al., 2012; Hamann et al., 2021a), high-elevation populations could be at increased risk of decline owing to novel herbivore stresses. We hypothesize that continued climate change will favor novel suites of traits that do not currently exist in any natural *B. stricta* populations along elevational or latitudinal gradients, such as the rapid flowering phenology of high-elevation/latitude populations combined with the drought tolerance and resistance to insect herbivory of low-elevation/latitude populations (Anderson et al., 2012, 2015; Wadgymar et al., 2017; Carley et al., 2021). *Boechera* species provide powerful study systems with which to examine how climate change is altering selection and evolutionary dynamics, especially under novel biotic interactions.

Rare species could be particularly prone to extinction under climate change (Enquist et al., 2019). Comparisons of geographically restricted vs. widespread *Boechera* species (Lovell and McKay, 2015) will yield insights into the population persistence of rare species under climate change. In *B. stricta*, we have already documented accelerated flowering phenologies, population declines in the trailing

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

edge and expansions in the leading edge, novel selection, and disrupted local adaptation from climate change. Similar approaches in rare and endangered species (e.g., *B. crandallii*, *B. vivariensis*, and *B. fecunda*) could predict extinction risks under climate change and guide conservation efforts. Even when extensive field research programs are not feasible in very rare endemic species, population genomic, greenhouse, and growth chamber studies can still illuminate the extent of genetic variation and adaptive potential under novel conditions.

CONCLUSIONS

Boechera populations occupy heterogeneous, relatively undisturbed habitats where short geographic distances are associated with large changes in abiotic and biotic environments. Thus, evolutionary patterns in *Boechera* offer key insight into evolutionary processes playing out in the natural habitat in which it has evolved. The experimental tractability of *Boechera* species allows researchers to address foundational questions in evolutionary genetics, including the consequences of reproductive variation on ecologically relevant traits, gene flow, and speciation, as well as emerging questions about adaptive dynamics through rapid environmental change. Numerous full siblings from inbred accessions and mapping populations can be transplanted into field gardens in diverse habitats to ascertain how agents of selection interact to shape evolution. Additionally, researchers can manipulate abiotic factors and biotic interactions—such as herbivore load—to test how these agents of selection interact to influence the evolution of complex traits under current climates and projected climate change. These manipulative experiments can dissect which factors drive the evolution of traits that serve multiple functions, such as glucosinolates, can interrogate the degree to which global change could impose new patterns of selection on natural populations and can generate robust predictions about population growth rates under projected climate change. Furthermore, these studies can illuminate whether increasing variability in conditions under climate change could favor phenotypic plasticity (Charmantier et al., 2008; Nicotra et al., 2010) while simultaneously quantifying the degree of genetic variation in plasticity through genotype by environment interactions. Complementing field research programs with genomic analyses can identify loci associated with adaptation and speciation, infer the evolutionary history of alleles at those loci, and potentially predict landscape-level responses to climate change by evaluating the fitness consequences of future climates for local alleles. As a result of its experimental tractability, available genomic resources, and unique suite of traits, the *Boechera* system offers an excellent complement to the diverse set of ecological model systems used in research today.

AUTHOR CONTRIBUTIONS

J.T.A. and T.M.O. conceived of the review topics. J.T.A., C.A.R., M.R.W., and T.M.O. wrote and edited the manuscript. C.A.R. created the figures.

ACKNOWLEDGMENTS

We thank Lauren Carley and Michael Windham for helpful discussion and comments on a previous draft. C.A.R. was supported by NSF award DEB-1753632 to Y. Brandvain, J. Ross-Ibarra, and M.M.S. Evans. J.T.A. was supported by the U.S. National Science Foundation (DEB-1553408 and DEB-1655732). M.R.W. was supported by grants from NSF (OIA-1656006, IOS-2016351) and matching funds from the State of Kansas through the Kansas Board of Regents. T.M.O. was supported by grants from NSF (EF-0723447) and the National Institutes of Health (GM086496). We are grateful to Susan Mazer and two reviewers for comments on a previous version. This paper is dedicated to David Siemens, a respected *Boechera* colleague and good friend, who passed away on 12 May 2022.

DATA AVAILABILITY STATEMENT

Updated DNA sequence data is referenced in Wang et al. (2019b) and Carley et al. (2021). Data and scripts for all published studies are available in the repositories listed in each paper. Seeds from the *B. stricta* GWAS population are available from the Arabidopsis Biological Resource Center.

ORCID

Jill T. Anderson http://orcid.org/0000-0002-3253-8142

REFERENCES

Alexander, J. M., J. M. Diez, and J. M. Levine. 2015a. Novel competitors shape species' responses to climate change. *Nature* 525: 515–518.

Alexander, P. J., M. D. Windham, J. B. Beck, I. A. Al-Shehbaz, L. Allphin, and C. D. Bailey. 2013. Molecular phylogenetics and taxonomy of the genus *Boechera* and related genera (Brassicaceae: Boechereae). *Systematic Botany* 38: 192–209.

Alexander, P. J., M. D. Windham, J. B. Beck, I. A. Al-Shehbaz, L. Allphin, and C. D. Bailey. 2015b. Weaving a tangled web: divergent and reticulate speciation in *Boechera fendleri* sensu lato (Brassicaceae: Boechereae). *Systematic Botany* 40: 572–596.

Alexandre, N. M., D. Haji, M. Bakhtiari, K. Chatla, J. M. Aguilar, K. Arzumanova, and N. K. Whiteman. 2022. A reference genome assembly of hybrid-derived california wild radish (*Raphanus sativus* × *raphanistrum*). *Journal of Heredity* 113: 197–204.

Alonso-Blanco, C., J. Andrade, C. Becker, F. Bemm, J. Bergelson, K. M. Borgwardt, J. Cao, et al. 2016. 1,135 Genomes reveal the global pattern of polymorphism in *Arabidopsis thaliana*. *Cell* 166: 481–491.

Alpert, P., and E. L. Simms. 2002. The relative advantages of plasticity and fixity in different environments: When is it good for a plant to adjust? *Evolutionary Ecology* 16: 285–297.

Amiteye, S., J. M. Corral, H. Vogel, and T. F. Sharbel. 2011. Analysis of conserved microRNAs in floral tissues of sexual and apomictic *Boechera* species. *BMC Genomics* 12: 500.

Anderson, J. T., and Z. J. Gezon. 2015. Plasticity in functional traits in the context of climate change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae). *Global Change Biology* 21: 1689–1703.

Anderson, J., D. Inouye, A. McKinney, R. Colautti, and T. Mitchell-Olds. 2012. Phenotypic plasticity and adaptive evolution

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society, B, Biological Sciences* 279: 3843–3852.

Anderson, J., C.-R. Lee, and T. Mitchell-Olds. 2010. Life history QTLs and natural selection on flowering time in *Boechera stricta*, a perennial relative of *Arabidopsis*. *Evolution* 65: 771–787.

Anderson, J., C.-R. Lee, and T. Mitchell-Olds. 2014. Strong selection genome-wide enhances fitness tradeoffs across environments and episodes of selection. *Evolution* 68: 16–31.

Anderson, J., N. Perera, B. Chowdhury, and T. Mitchell-Olds. 2015. Microgeographic patterns of genetic divergence and adaptation across environmental gradients in *Boechera stricta* (Brassicaceae). *American Naturalist* 186: S60–S73.

Anderson, J. T., M. I. Jameel, and M. A. Geber. 2021. Selection favors adaptive plasticity in a long-term reciprocal transplant experiment. *Evolution* 75: 1711–1726.

Anderson, J. T., C.-R. Lee, C. A. Rushworth, R. I. Colautti, and T. Mitchell-Olds. 2013. Genetic trade-offs and conditional neutrality contribute to local adaptation. *Molecular Ecology* 22: 699–708.

Anderson, J. T., and S. M. Wadgymar. 2020. Climate change disrupts local adaptation and favours upslope migration. *Ecology Letters* 23: 181–192.

Armbruster, W. S. 1993. *Dalechampia*. Flora of North America north of Mexico, vol. 12, Flora of North America Editorial Committee [eds.]. Oxford University Press, NY, NY, USA; Oxford, UK. Website: http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=109241

Armbruster, W. S., J. Lee, and B. G. Baldwin. 2009. Macroevolutionary patterns of defense and pollination in *Dalechampia* vines: Adaptation, exaptation, and evolutionary novelty. *Proceedings of the National Academy of Sciences, USA* 106: 18085–18090.

Arro, J., and J. A. Labate. 2022. Genetic variation in a radish (*Raphanus sativus* L.) geodiversity collection. *Genetic Resources and Crop Evolution* 69: 163–171.

Asker, S., and L. Jerling. 1992. Apomixis in plants. CRC Press, Boca Raton, FL, USA.

Atwell, S., Y. S. Huang, B. J. Vilhjálmsson, G. Willems, M. Horton, Y. Li, D. Meng, et al. 2010. Genome-wide association study of 107 phenotypes in *Arabidopsis thaliana* inbred lines. *Nature* 465: 627–631.

Auge, G. A., S. Penfield, and K. Donohue. 2019. Pleiotropy in developmental regulation by flowering-pathway genes: is it an evolutionary constraint? *New Phytologist* 224: 55–70.

Bartomeus, I., M. Vilà, and I. Steffan-Dewenter. 2010. Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *Journal of Ecology* 98: 440–450.

Baucom, R. S., S.-M. Chang, J. M. Kniskern, M. D. Rausher, and J. R. Stinchcombe. 2011. Morning glory as a powerful model in ecological genomics: tracing adaptation through both natural and artificial selection. *Heredity* 107: 377–385.

Beardsley, P. M., S. E. Schoenig, J. B. Whittall, and R. G. Olmstead. 2004. Patterns of evolution in western North American *Mimulus* (Phrymaceae). *American Journal of Botany* 91: 474–489.

Beck, J. B., P. J. Alexander, L. Allphin, I. A. Al-Shehbaz, C. Rushworth, C. D. Bailey, and M. D. Windham. 2012. Does hybridization drive the transition to asexuality in diploid *Boechera*? *Evolution* 66: 985–995.

Becklin, K. M., J. T. Anderson, L. M. Gerhart, S. M. Wadgymar, C. A. Wessinger, and J. K. Ward. 2016. Examining plant physiological responses to climate change through an evolutionary lens. *Plant Physiology* 172: 635–649.

Beilstein, M. A., N. S. Nagalingum, M. D. Clements, S. R. Manchester, and S. Mathews. 2010. Dated molecular phylogenies indicate a Miocene origin for *Arabidopsis thaliana*. *PNAS* 107: 18724–18728.

Bell, G. 1980. The costs of reproduction and their consequences. *American Naturalist* 116: 45–76.

Bemmels, J. B., and J. T. Anderson. 2019. Climate change shifts natural selection and the adaptive potential of the perennial forb *Boechera stricta* in the Rocky Mountains. *Evolution* 73: 2247–2262.

Ben-David, U., and A. Amon. 2020. Context is everything: aneuploidy in cancer. *Nature Reviews Genetics* 21: 44–62.

Benedito, V. A., I. Torres-Jerez, J. D. Murray, A. Andriankaja, S. Allen, K. Kakar, M. Wandrey, et al. 2008. A gene expression atlas of the model legume *Medicago truncatula*. *Plant Journal* 55: 504–513.

Bernasconi, G., J. Antonovics, A. Biere, D. Charlesworth, L. F. Delph, D. Filatov, T. Giraud, et al. 2009. *Silene* as a model system in ecology and evolution. *Heredity* 103: 5–14.

Blair, A. C., and L. M. Wolfe. 2004. The evolution of an invasive plant: an experimental study with *Silene latifolia*. *Ecology* 85: 3035–3042.

Brachi, B., N. Faure, M. Horton, E. Flahauw, A. Vazquez, M. Nordborg, J. Bergelson, et al. 2010. Linkage and association mapping of *Arabidopsis thaliana* flowering time in nature. *PLoS Genetics* 6: e1000940.

Brachi, B., C. G. Meyer, R. Villoutreix, A. Platt, T. C. Morton, F. Roux, and J. Bergelson. 2015. Coselected genes determine adaptive variation in herbivore resistance throughout the native range of *Arabidopsis thaliana*. *PNAS* 112: 4032–4037.

Brandvain, Y., A. M. Kenney, L. Flagel, G. Coop, and A. L. Sweigart. 2014. Speciation and introgression between *Mimulus nasutus* and *Mimulus guttatus*. *PLoS Genetics* 10: e1004410.

Bressan, M., M.-A. Roncato, F. Bellvert, G. Comte, F. el Z. Haichar, W. Achouak, and O. Berge. 2009. Exogenous glucosinolate produced by *Arabidopsis thaliana* has an impact on microbes in the rhizosphere and plant roots. *ISME Journal* 3: 1243–1257.

Brukhin, V., J. V. Osadtchiy, A. M. Florez-Rueda, D. Smetanin, E. Bakin, M. S. Nobre, and U. Grossniklaus. 2019. The *Boechera* genus as a resource for apomixis research. *Frontiers in Plant Science* 10: 392.

Cabin, Z., N. J. Derieg, A. Garton, T. Ngo, A. Quezada, C. Gasseholm, M. Simon, and S. A. Hodges. 2022. Non-pollinator selection for a floral homeotic mutant conferring loss of nectar reward in *Aquilegia coerulea*. *Current Biology* 32: 1332-1341.e5.

Campbell, D. R. 2019. Early snowmelt projected to cause population decline in a subalpine plant. *Proceedings of the National Academy of Sciences, USA* 116: 12901–12906.

Campbell, D. R., M. Bischoff, R. A. Raguso, H. M. Briggs, and P. Sosenski. 2022. Selection of floral traits by pollinators and seed predators during sequential life history stages. *The American Naturalist* 199: 808–823.

Cano, L. M., S. Raffaele, R. H. Haugen, D. G. O. Saunders, L. Leonelli, D. MacLean, S. A. Hogenhout, and S. Kamoun. 2013. Major transcriptome reprogramming underlies floral mimicry induced by the rust fungus *Puccinia monoica* in *Boechera stricta*. *PLoS ONE* 8: e75293.

Carley, L. N., J. P. Mojica, B. Wang, C.-Y. Chen, Y.-P. Lin, K. V. S. K. Prasad, E. Chan, et al. 2021. Ecological factors influence balancing selection on leaf chemical profiles of a wildflower. *Nature Ecology & Evolution* 5: 1135–1144.

Carley, L. N., W. F. Morris, R. Walsh, D. L. Riebe, and T. Mitchell-Olds. 2022. Are genetic variation and demographic performance linked? *Biological Conservation*. https://doi.org/10.1111/eva.13487

Carman, J. G. 1997. Asynchronous expression of duplicate genes in angiosperms may cause apomixis, bispory, tetraspory, and polyembryony. *Biological Journal of the Linnean Society* 61: 51–94.

Carman, J. G., M. Mateo de Arias, L. Gao, X. Zhao, B. M. Kowallis, D. A. Sherwood, M. K. Srivastava, et al. 2019. Apospory and diplospory in diploid *Boechera* (Brassicaceae) may facilitate speciation by recombination-driven apomixis-to-sex reversals. *Frontiers in Plant Science* 10: 724.

Charlesworth, B. 2015. Causes of natural variation in fitness: evidence from studies of *Drosophila* populations. *Proccedings of the National Academy of Sciences, USA* 112: 1662–1669.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320: 800–803.

Clark, R. M., G. Schweikert, C. Toomajian, S. Ossowski, G. Zeller, P. Shinn, N. Warthmann, et al. 2007. Common sequence polymorphisms shaping genetic diversity in *Arabidopsis thaliana*. *Science* 317: 338–342.

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Coberly, L. C., and M. D. Rausher. 2003. Analysis of a chalcone synthase mutant in *Ipomoea purpurea* reveals a novel function for flavonoids: amelioration of heat stress. *Molecular Ecology* 12: 1113–1124.

Colautti, R. I., J. Ågren, and J. T. Anderson. 2017. Phenological shifts of native and invasive species under climate change: insights from the *Boechera–Lythrum* model. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 372: 20160032.

Conner, J. A., M. Mookkan, H. Huo, K. Chae, and P. Ozias-Akins. 2015. A parthenogenesis gene of apomict origin elicits embryo formation from unfertilized eggs in a sexual plant. *Proccedings of the National Academy of Sciences, USA* 112: 11205–11210.

Conner, J. K., C. J. Mills, V. A. Koelling, and K. Karoly. 2014. Artificial selection on anther exsertion in wild radish, *Raphanus raphanistrum*. *Scientific Data* 1: 140027.

Conner, J., and S. Via. 1993. Patterns of phenotypic and genetic correlations among morphological and life-history traits in wild radish, *Raphanus raphanistrum*. *Evolution* 47: 704–711.

Corral, J. M., H. Vogel, O. M. Aliyu, G. Hensel, T. Thiel, J. Kumlehn, and T. F. Sharbel. 2013. A conserved apomixis-specific polymorphism is correlated with exclusive exonuclease expression in premeiotic ovules of apomictic *Boechera* Species. *Plant Physiology* 163: 1660–1672.

Davila Olivas, N. H., W. Kruijer, G. Gort, C. L. Wijnen, J. J. A. Loon, and M. Dicke. 2017. Genome-wide association analysis reveals distinct genetic architectures for single and combined stress responses in *Arabidopsis thaliana*. *New Phytologist* 213: 838–851.

Day, P. D., J. Pellicer, and R. G. Kynast. 2012. Orange balsam (*Impatiens capensis* Meerb., Balsaminaceae): a re-evaluation by chromosome number and genome size. *Journal of the Torrey Botanical Society* 139: 26–33.

De Kort, H., B. Panis, K. Helsen, R. Douzet, S. B. Janssens, and O. Honnay. 2020. Pre-adaptation to climate change through topography-driven phenotypic plasticity. *Journal of Ecology* 108: 1465–1474.

De Maio, N., D. Schrempf, and C. Kosiol. 2015. PoMo: an allele frequency-based approach for species tree estimation. *Systematic Biology* 64: 1018–1031.

Delph, L. F., and J. K. Kelly. 2014. On the importance of balancing selection in plants. *New Phytologist* 201: 45–56.

DeMarche, M. L., D. F. Doak, and W. F. Morris. 2018. Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. *Global Change Biology* 24: 1614–1625.

Descombes, P., C. Pitteloud, G. Glauser, E. Defossez, A. Kergunteuil, P.-M. Allard, S. Rasmann, and L. Pellissier. 2020. Novel trophic interactions under climate change promote alpine plant coexistence. *Science* 370: 1469.

Donohue, K., and J. Schmitt. 1998. Maternal environmental effects in plants-adaptive plasticity? *In* T. A. Mousseau and C. W. Fox [eds.]. Maternal effects as adaptations, 137–158. Oxford University Press, Oxford, UK.

Dziasek, K., L. Simon, C. Lafon-Placette, B. Laenen, C. Wärdig, J. Santos-González, T. Slotte, and C. Köhler. 2021. Hybrid seed incompatibility in *Capsella* is connected to chromatin condensation defects in the endosperm. *PLoS Genetics* 17: e1009370.

Eckhart, V. M., I. Singh, A. M. Louthan, A. J. Keledjian, A. Chu, D. A. Moeller, and M. A. Geber. 2010. Plant-soil water relations and species border of *Clarkia xantiana* ssp. *xantiana* (Onagraceae). *International Journal of Plant Sciences* 171: 749–760.

Ellis, T. J., F. M. Postma, C. G. Oakley, and J. Ågren. 2021. Life-history trade-offs and the genetic basis of fitness in *Arabidopsis thaliana*. *Molecular Ecology* 30: 2846–2858.

Enquist, B. J., X. Feng, B. Boyle, B. Maitner, E. A. Newman, P. M. Jørgensen, P. R. Roehrdanz, et al. 2019. The commonness of rarity: global and future distribution of rarity across land plants. *Science Advances* 5: eaaz0414.

Etterson, J. R., and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* 294: 151–154.

Exposito-Alonso, M., H. A. Burbano, O. Bossdorf, R. Nielsen, and D. Weigel. 2019a. Natural selection on the *Arabidopsis thaliana* genome in present and future climates. *Nature* 573: 126–129.

Exposito-Alonso, M., M. Exposito-Alonso, R. Gómez Rodríguez, C. Barragán, G. Capovilla, E. Chae, J. Devos, et al. 2019b. Natural selection on the *Arabidopsis thaliana* genome in present and future climates. *Nature* 573: 126–129.

Fenster, C. B., and L. F. Galloway. 2000a. Inbreeding and outbreeding depression in natural populations of *Chamaecrista fasciculata* (Fabaceae). *Conservation Biology* 14: 1406–1412.

Fenster, C. B., and L. F. Galloway. 2000b. Population differentiation in an annual legume: genetic architecture. *Evolution* 54: 1157–1172.

Filatov, D. A., and S. Burke. 2004. DNA diversity in Hawaiian endemic plant *Schiedea globosa*. *Heredity* 92: 452–458.

Filiault, D. L., E. S. Ballerini, T. Mandáková, G. Aköz, N. J. Derieg, J. Schmutz, J. Jenkins, et al. 2018. The *Aquilegia* genome provides insight into adaptive radiation and reveals an extraordinarily polymorphic chromosome with a unique history. *eLife* 7: e36426.

Fior, S., M. Li, B. Oxelman, R. Viola, S. A. Hodges, L. Ometto, and C. Varotto. 2013. Spatiotemporal reconstruction of the *Aquilegia* rapid radiation through next-generation sequencing of rapidly evolving cp DNA regions. *New Phytologist* 198: 579–592.

Fournier-Level, A., A. Korte, M. D. Cooper, M. Nordborg, J. Schmitt, and A. M. Wilczek. 2011. A map of local adaptation in *Arabidopsis thaliana*. *Science* 334: 86–89.

Fournier-Level, A., M. A. Taylor, J. F. Paril, A. Martínez-Berdeja, M. C. Stitzer, M. D. Cooper, J. L. Roe, et al. 2022. Adaptive significance of flowering time variation across natural seasonal environments in *Arabidopsis thaliana*. *New Phytologist* 234: 719–734.

Franks, S. J. 2011. Plasticity and evolution in drought avoidance and escape in the annual plant *Brassica rapa*. *New Phytologist* 190: 249–257.

Franks, S. J., N. C. Kane, N. B. O'Hara, S. Tittes, and J. S. Rest. 2016. Rapid genome-wide evolution in *Brassica rapa* populations following drought revealed by sequencing of ancestral and descendant gene pools. *Molecular Ecology* 25: 3622–3631.

Franks, S. J., S. Sim, and A. E. Weis. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences, USA* 104: 1278–1282.

Friesen, M. L., M. A. Cordeiro, R. V. Penmetsa, M. Badri, T. Huguet, M. E. Aouani, D. R. Cook, and S. V. Nuzhdin. 2010. Population genomic analysis of Tunisian *Medicago truncatula* reveals candidates for local adaptation: population genomics of *Medicago truncatula*. *Plant Journal* 63: 623–635.

Friesen, M. L., E. J. von Wettberg, M. Badri, K. S. Moriuchi, F. Barhoumi, P. L. Chang, S. Cuellar-Ortiz, et al. 2014. The ecological genomic basis of salinity adaptation in Tunisian *Medicago truncatula*. *BMC Genomics* 15: 1160.

Fyfe, J. C., C. Derksen, L. Mudryk, G. M. Flato, B. D. Santer, N. C. Swart, N. P. Molotch, et al. 2017. Large near-term projected snowpack loss over the western United States. *Nature Communications* 8: 14996.

Galloway, L. F. 2005. Maternal effects provide phenotypic adaptation to local environmental conditions. *New Phytologist* 166: 93–100.

Galloway, L. F., and J. R. Etterson. 2007. Transgenerational plasticity is adaptive in the wild. *Science* 318: 1134–1136.

Galloway, L. F., and C. Fenster. 2000. Population differentiation in an annual legume: Local adaptation. *Evolution* 54: 1173–1181.

Gasch, A. P., B. A. Payseur, and J. E. Pool. 2016. The power of natural variation for model organism biology. *Trends in Genetics* 32: 147–154.

Geber, M. A., and V. M. Eckhart. 2005. Experimental studies of adaptation in *Clarkia xantiana*: II. Fitness variation across a subspecies border. *Evolution* 59: 521–531.

Goldstein, B., and N. King. 2016. The future of cell biology: emerging model organisms. *Trends in Cell Biology* 26: 818–824.

Gould, B., D. A. Moeller, V. M. Eckhart, P. Tiffin, E. Fabio, and M. A. Geber. 2014. Local adaptation and range boundary formation in response to complex environmental gradients across the

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

geographical range of *Clarkia xantiana* ssp. *xantiana*. *Journal of Ecology* 102: 95–107.

Guo, Y.-L., J. S. Bechsgaard, T. Slotte, B. Neuffer, M. Lascoux, D. Weigel, and M. H. Schierup. 2009. Recent speciation of *Capsella rubella* from *Capsella grandiflora*, associated with loss of self-incompatibility and an extreme bottleneck. *Proceedings of the National Academy of Sciences, USA* 106: 5246–5251.

Gupta, S., A. Harkess, A. Soble, M. Van Etten, J. Leebens-Mack, and R. S. Baucom. 2021. Inter-chromosomal linkage disequilibrium and linked fitness cost loci associated with selection for herbicide resistance. *bioRxiv*. https://doi.org/10.1101/2021.04.04.438381 [Preprint].

Halkier, B. A., and J. Gershenzon. 2006. Biology and biochemistry of glucosinolates. *Annual Review of Plant Biology* 57: 303–333.

Hall, M. C., and J. H. Willis. 2006. Divergent selection on flowering time contributes to local adaptation in *Mimulus guttatus* populations. *Evolution* 60: 2466–2477.

Hall, M. C., D. B. Lowry, and J. H. Willis. 2010. Is local adaptation in *Mimulus guttatus* caused by trade-offs at individual loci? Trade-offs can contribute to adaptation in *Mimulus*. *Molecular Ecology* 19: 2739–2753.

Hamann, E., C. Blevins, S. J. Franks, M. I. Jameel, and J. T. Anderson. 2021a. Climate change alters plant–herbivore interactions. *New Phytologist* 229: 1894–1910.

Hamann, E., S. M. Wadgymar, and J. T. Anderson. 2021b. Costs of reproduction under experimental climate change across elevations in the perennial forb *Boechera stricta*. *Proceedings of the Royal Society B: Biological Sciences* 288: rspb.2020.3134, 20203134.

Hamann, E., A. E. Weis, and S. J. Franks. 2018. Two decades of evolutionary changes in *Brassica rapa* in response to fluctuations in precipitation and severe drought. *Evolution* 72: 2682–2696.

Hamilton, J. A., M. Okada, T. Korves, and J. Schmitt. 2015. The role of climate adaptation in colonization success in *Arabidopsis thaliana*. *Molecular Ecology* 24: 2253–2263.

Hendriks, K. P., T. Mandáková, N. M. Hay, E. Ly, A. Hooft van Huysduynen, R. Tamrakar, S. K. Thomas, et al. 2021. The best of both worlds: combining lineage-specific and universal bait sets in target-enrichment hybridization reactions. *Applications in Plant Sciences* 9: aps3.11438.

Hendry, A. P. 2015. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *Journal of Heredity* 107: 25–41.

Hereford, J. 2009. A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist* 173: 579–588.

Heschel, M. S., N. Hausmann, and J. Schmitt. 2005. Testing for stress-dependent inbreeding depression in *Impatiens capensis* (Balsaminaceae). *American Journal of Botany* 92: 1322–1329.

Hestrin, R., P. K. Weber, J. Pett-Ridge, and J. Lehmann. 2021. Plants and mycorrhizal symbionts acquire substantial soil nitrogen from gaseous ammonia transport. *New Phytologist* 231: 1746–1757.

Hibbins, M. S., and M. W. Hahn. 2021. The effects of introgression across thousands of quantitative traits revealed by gene expression in wild tomatoes. *PLoS Genetics* 17: e1009892.

Hojsgaard, D., S. Klatt, R. Baier, J. G. Carman, and E. Hörandl. 2014. Taxonomy and biogeography of apomixis in angiosperms and associated biodiversity characteristics. *Critical Reviews in Plant Sciences* 33: 414–427.

Hooker, J. 1908. Les especes du genre '*Impatiens*' dans l'herbier du Museum de Paris. *Nouvelles Archives du Muséum d'Histoire Naturelle Paris* 10: 233–272.

Hopkins, R. J., N. M. van Dam, and J. J. A. van Loon. 2009. Role of glucosinolates in insect–plant relationships and multitrophic interactions. *Annual Review of Entomology* 54: 57–83.

Hörandl, E. 2006. The complex causality of geographical parthenogenesis. *New Phytologist* 171: 525–538.

Hossain, M. S., W. Ye, M. A. Hossain, E. Okuma, M. Uraji, Y. Nakamura, I. C. Mori, and Y. Murata. 2013. Glucosinolate degradation products, isothiocyanates, nitriles, and thiocyanates, induce stomatal closure accompanied by peroxidase-mediated reactive oxygen species production in *Arabidopsis thaliana*. *Bioscience, Biotechnology, and Biochemistry* 77: 977–983.

Huang, W., R. F. Lyman, R. A. Lyman, M. A. Carbone, S. T. Harbison, M. M. Magwire, and T. F. Mackay. 2016. Spontaneous mutations and the origin and maintenance of quantitative genetic variation. *eLife* 5: e14625.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353–362.

Jiang, Y., M. Wang, R. Zhang, J. Xie, X. Duan, H. Shan, G. Xu, and H. Kong. 2020. Identification of the target genes of AqAPETALA3-3 (AqAP3-3) in *Aquilegia coerulea* (Ranunculaceae) helps understand the molecular bases of the conserved and nonconserved features of petals. *New Phytologist* 227: 1235–1248.

Jordon-Thaden, I. E., J. B. Beck, C. A. Rushworth, M. D. Windham, N. Diaz, J. T. Cantley, C. T. Martine, and C. J. Rothfels. 2020. A basic ddRADseq two-enzyme protocol performs well with herbarium and silica-dried tissues across four genera. *Applications in Plant Sciences* 8: e11344.

Kane, N. C., J. M. Burke, L. Marek, G. Seiler, F. Vear, G. Baute, S. J. Knapp, and P. Vincourt. 2013. Sunflower genetic, genomic and ecological resources. *Molecular Ecology Resources* 13: 10–20.

Kantama, L., T. F. Sharbel, M. E. Schranz, T. Mitchell-Olds, S. de Vries, and H. de Jong. 2007. Diploid apomicts of the *Boechera holboellii* complex display large-scale chromosome substitutions and aberrant chromosomes. *Proceedings of the National Academy of Sciences, USA* 104: 14026–14031.

Kapralov, M. V., M. Stift, and D. A. Filatov. 2009. Evolution of genome size in Hawaiian endemic genus *Schiedea* (Caryophyllaceae). *Tropical Plant Biology* 2: 77–83.

Karasov, T. L., J. M. Kniskern, L. Gao, B. J. DeYoung, J. Ding, U. Dubiella, R. O. Lastra, et al. 2014. The long-term maintenance of a resistance polymorphism through diffuse interactions. *Nature* 512: 436–440.

Katz, E., J.-J. Li, B. Jaegle, H. Ashkenazy, S. R. Abrahams, C. Bagaza, S. Holden, et al. 2021. Genetic variation, environment and demography intersect to shape *Arabidopsis* defense metabolite variation across Europe. *eLife* 10: e67784.

Kaur, S., C. Atri, J. Akhatar, M. Mittal, R. Kaur, and S. S. Banga. 2021. Genetics of days to flowering, maturity and plant height in natural and derived forms of *Brassica rapa* L. *Theoretical and Applied Genetics* 134: 473–487.

Ke, F., L. Vasseur, H. Yi, L. Yang, X. Wei, B. Wang, and M. Kang. 2021. Gene flow, linked selection, and divergent sorting of ancient polymorphism shape genomic divergence landscape in a group of edaphic specialists. *Molecular Ecology* 31: 104-118.

Keith, R. A., and T. Mitchell-Olds. 2019. Antagonistic selection and pleiotropy constrain the evolution of plant chemical defenses. *Evolution* 73: 947–960.

Kenney, A. M., and A. L. Sweigart. 2016. Reproductive isolation and introgression between sympatric *Mimulus* species. *Molecular Ecology* 25: 2499–2517.

Khanday, I., D. Skinner, B. Yang, R. Mercier, and V. Sundaresan. 2019. A male-expressed rice embryogenic trigger redirected for asexual propagation through seeds. *Nature* 565: 91–95.

Kiefer, C., C. Dobeš, T. Sharbel, and M. Koch. 2009. Phylogeographic structure of the chloroplast DNA gene pool in North American *Boechera* – A genus and continental-wide perspective. *Molecular Phylogenetics and Evolution* 52: 303–311.

Kinoshita, A., and R. Richter. 2020. Genetic and molecular basis of floral induction in *Arabidopsis thaliana*. *Journal of Experimental Botany* 71: 2490–2504.

Kitashiba, H., and J. B. Nasrallah. 2014. Self-incompatibility in Brassicaceae crops: lessons for interspecific incompatibility. *Breeding Science* 64: 23–37.

Kliver, S., M. Rayko, A. Komissarov, E. Bakin, D. Zhernakova, K. Prasad, C. Rushworth, et al. 2018. Assembly of the *Boechera retrofracta* genome and evolutionary analysis of apomixis-associated genes. *Genes* 9: E185.

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Koenig, D., J. Hagmann, R. Li, F. Bemm, T. Slotte, B. Neuffer, S. I. Wright, and D. Weigel. 2019. Long-term balancing selection drives evolution of immunity genes in *Capsella*. *eLife* 8: e43606.

Körner, C. 2007. The use of altitude in ecological research. *Trends in Ecology & Evolution* 22: 569–574.

Kramer, E. M. 2009. *Aquilegia*: a new model for plant development, ecology, and evolution. *Annual Review of Plant Biology* 60: 261–277.

Kramer, E. M., and S. A. Hodges. 2010. *Aquilegia* as a model system for the evolution and ecology of petals. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 365: 477-490.

Kuester, A., A. Wilson, S. Chang, and R. S. Baucom. 2016. A resurrection experiment finds evidence of both reduced genetic diversity and potential adaptive evolution in the agricultural weed *Ipomoea purpurea*. *Molecular Ecology* 25: 4508–4520.

Küster, H., A. Becker, D. Samac, and M. Tesfaye eds. 2006. Transcriptomics. *In* U. Mathesius, E. P. Journet, and L. W. Sumner [eds.]. The Medicago truncatula handbook. Noble Research Institute, Ardmore, OK, USA. Website: http://www.noble.org/medicago-handbook/

Lafon-Placette, C., M. R. Hatorangan, K. A. Steige, A. Cornille, M. Lascoux, T. Slotte, and C. Köhler. 2018. Paternally expressed imprinted genes associate with hybridization barriers in *Capsella*. *Nature Plants* 4: 352–357.

Leamy, L. J., C. Lee, V. Cousins, I. Mujacic, A. J. Manzaneda, K. Prasad, T. Mitchell-Olds, and B. Song. 2014. Large-scale adaptive divergence in *Boechera fecunda*, an endangered wild relative of *Arabidopsis*. *Ecology and Evolution* 4: 3175–3186.

Lee, C. R., and T. Mitchell-Olds. 2011. Quantifying effects of environmental and geographical factors on patterns of genetic differentiation. *Molecular Ecology* 20: 4631–4642.

Lee, C.-R., and T. Mitchell-Olds. 2013. Complex trait divergence contributes to environmental niche differentiation in ecological speciation of *Boechera stricta*. *Molecular Ecology* 22: 2204–2217.

Lee, C.-R., B. Wang, J. P. Mojica, T. Mandáková, K. V. S. K. Prasad, J. L. Goicoechea, N. Perera, et al. 2017. Young inversion with multiple linked QTLs under selection in a hybrid zone. *Nature Ecology & Evolution* 1: 119.

Levins, R. 1963. Theory of fitness in a heterogeneous environment. ii. developmental flexibility and niche selection. *American Naturalist* 97: 75–90.

Lexer, C., M. Welch, J. Durphy, and L. H. Rieseberg. 2003. Natural selection for salt tolerance quantitative trait loci (QTLs) in wild sunflower hybrids: Implications for the origin of *Helianthus paradoxus*, a diploid hybrid species. *Molecular Ecology* 12: 1225–1235.

Li, F.-W., C. A. Rushworth, J. B. Beck, and M. D. Windham. 2017. *Boechera* microsatellite website: an online portal for species identification and determination of hybrid parentage. *Database* 2016: 1–11.

Lin, Y.-P., T. Mitchell-Olds, and C.-R. Lee. 2021. The ecological, genetic and genomic architecture of local adaptation and population differentiation in *Boechera stricta*. *Proceedings of the Royal Society, B, Biological Sciences* 288: 20202472.

Lively, C. M., and L. T. Morran. 2014. The ecology of sexual reproduction. *Journal of Evolutionary Biology* 27: 1292–1303.

Lovell, J. T., O. M. Aliyu, M. Mau, M. E. Schranz, M. Koch, C. Kiefer, B.-H. Song, et al. 2013. On the origin and evolution of apomixis in *Boechera*. *Plant Reproduction* 26: 309–315.

Lovell, J. T., K. Grogan, T. F. Sharbel, and J. K. McKay. 2014. Mating system and environmental variation drive patterns of adaptation in *Boechera spatifolia* (Brassicaceae). *Molecular Ecology* 23: 4486–4497.

Lovell, J. T., J. Jenkins, D. B. Lowry, S. Mamidi, A. Sreedasyam, X. Weng, K. Barry, et al. 2018. The genomic landscape of molecular responses to natural drought stress in *Panicum hallii*. *Nature Communications* 9: 5213.

Lovell, J. T., A. H. MacQueen, S. Mamidi, J. Bonnette, J. Jenkins, J. D. Napier, A. Sreedasyam, et al. 2021. Genomic mechanisms of climate adaptation in polyploid bioenergy switchgrass. *Nature* 590: 438–444.

Lovell, J. T., and J. K. McKay. 2015. Ecological genetics of range size variation in *Boechera* spp. (Brassicaceae). *Ecology and Evolution* 5: 4962–4975.

Lovell, J. T., R. J. Williamson, S. I. Wright, J. K. McKay, and T. F. Sharbel. 2017. Mutation accumulation in an asexual relative of *Arabidopsis*. *PLoS Genetics* 13: e1006550.

Lowry, D. B., D. Popovic, D. J. Brennan, and L. M. Holeski. 2019. Mechanisms of a locally adaptive shift in allocation among growth, reproduction, and herbivore resistance in *Mimulus guttatus*. *Evolution* 73: 1168–1181.

Lowry, D. B., R. C. Rockwood, and J. H. Willis. 2008. Ecological reproductive isolation of coast and inland races of *Mimulus guttatus*. *Evolution* 62: 2196–2214.

Lowry, D. B., and J. H. Willis. 2010. A widespread chromosomal inversion polymorphism contributes to a major life-history transition, local adaptation, and reproductive isolation. *PLoS Biology* 8: e1000500.

Mabry, M. E., S. D. Turner-Hissong, E. Y. Gallagher, A. C. McAlvay, H. An, P. P. Edger, J. D. Moore, et al. 2021. The evolutionary history of wild, domesticated, and feral *Brassica oleracea* (Brassicaceae). *Molecular Biology and Evolution* 38: 4419–4434.

MacTavish, R., and J. T. Anderson. 2020. Resource availability alters fitness trade-offs: implications for evolution in stressful environments. *American Journal of Botany* 107: 308–318.

MacTavish, R., and J. T. Anderson. 2022. Water and nutrient availability exert selection on reproductive phenology. *American Journal of Botany* https://doi.org/10.1002/ajb2.16057

Mandáková, T., P. Hloušková, M. D. Windham, T. Mitchell-Olds, K. Ashby, B. Price, J. Carman, and M. A. Lysak. 2020. Chromosomal evolution and apomixis in the cruciferous tribe Boechereae. *Frontiers in Plant Science* 11: 514.

Mandáková, T., M. E. Schranz, T. F. Sharbel, H. de Jong, and M. A. Lysak. 2015. Karyotype evolution in apomictic *Boechera* and the origin of the aberrant chromosomes. *Plant Journal* 82: 785–793.

Masson-Delmotte, V., P. Zhai, S. Pirani, L. Connors, C. Péan, S. Berger, N. Caud, et al. 2021. IPCC, 2021: Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Mau, M., J. M. Corral, H. Vogel, M. Melzer, J. Fuchs, M. Kuhlmann, N. De Storme, et al. 2013. The conserved chimeric transcript *UPGRADE2* is associated with unreduced pollen formation and is exclusively found in apomictic *Boechera* species. *Plant Physiology* 163: 1640–1659.

Mau, M., T. Liiving, L. Fomenko, R. Goertzen, D. Paczesniak, L. Böttner, and T. F. Sharbel. 2021. The spread of infectious asexuality through haploid pollen. *New Phytologist* 230: 804–820.

Mau, M., J. T. Lovell, J. M. Corral, C. Kiefer, M. A. Koch, O. M. Aliyu, and T. F. Sharbel. 2015. Hybrid apomicts trapped in the ecological niches of their sexual ancestors. *Proceedings of the National Academy of Sciences, USA* 112: E2357–E2365.

Maynard Smith, J. 1978. The evolution of sex. Cambridge University Press, Cambridge, UK.

McCall, C., D. M. Waller, and T. Mitchell-Olds. 1994. Effects of serial inbreeding on fitness components in *Impatiens capensis*. *Evolution* 48: 818–827.

Min, Y., and E. M. Kramer. 2020. Transcriptome profiling and weighted gene co-expression network analysis of early floral development in *Aquilegia coerulea*. *Scientific Reports* 10: 19637.

Moeller, D. A. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85: 3289–3301.

Moghe, G. D., D. E. Hufnagel, H. Tang, Y. Xiao, I. Dworkin, C. D. Town, J. K. Conner, and S.-H. Shiu. 2014. Consequences of whole-genome triplication as revealed by comparative genomic analyses of the wild radish *Raphanus raphanistrum* and three other Brassicaceae species. *Plant Cell* 26: 1925–1937.

Monnahan, P. J., J. Colicchio, L. Fishman, S. J. Macdonald, and J. K. Kelly. 2021. Predicting evolutionary change at the DNA level in a natural *Mimulus* population. *PLoS Genetics* 17: e1008945.

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Monroe, J. G., T. Srikant, P. Carbonell-Bejerano, C. Becker, M. Lensink, M. Exposito-Alonso, M. Klein, et al. 2022. Mutation bias reflects natural selection in *Arabidopsis thaliana*. *Nature* 602: 101–105.

Morales-Briones, D. F., N. Lin, E. Y. Huang, D. L. Grossenbacher, J. M. Sobel, C. D. Gilmore, D. C. Tank, and Y. Yang. 2022. Phylogenomic analyses in Phrymaceae reveal extensive gene tree discordance in relationships among major clades. *American Journal of Botany* 109: 1035–1046.

Moran, N. A. 1992. The evolutionary maintenance of alternative phenotypes. *Evolution* 139: 971–989.

Morin, D. P., P. J. Alexander, J. B. Beck, M. D. Windham, and C. D. Bailey. 2018. Deciphering the sexual diploid members of the *Boechera suffrutescens* complex (Brassicaceae, Boechereae). *PhytoKeys* 98: 15–50.

Morris, W. F., and D. F. Doak. 1998. Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *American Journal of Botany* 85: 784–793.

Mountain Research Initiative. 2015. Elevation-dependent warming in mountain regions of the world. *Nature Climate Change* 5: 424–430.

Moyle, L. C. 2008. Ecological and evolutionary genomics in the wild tomatoes (*Solanum* sect. *Lycopersicon*). *Evolution* 62: 2995–3013.

Mun, J.-H., H. Chung, W.-H. Chung, M. Oh, Y.-M. Jeong, N. Kim, B. O. Ahn, et al. 2015. Construction of a reference genetic map of *Raphanus sativus* based on genotyping by whole-genome resequencing. *Theoretical and Applied Genetics* 128: 259–272.

Napier, J. D., P. P. Grabowski, J. T. Lovell, J. Bonnette, S. Mamidi, M. J. Gomez-Hughes, A. VanWallendael, et al. 2022. A generalist–specialist trade-off between switchgrass cytotypes impacts climate adaptation and geographic range. *Proceedings of the National Academy of Sciences, USA* 119: e2118879119.

Navarro, J., J. M. Powers, A. Paul, and D. R. Campbell. 2022. Phenotypic plasticity and selection on leaf traits in response to snowmelt timing and summer precipitation. *New Phytologist* 234: 1477–1490.

Ni, M., M. Feretzaki, W. Li, A. Floyd-Averette, P. Mieczkowski, F. S. Dietrich, and J. Heitman. 2013. Unisexual and heterosexual meiotic reproduction generate aneuploidy and phenotypic diversity de novo in the yeast *Cryptococcus neoformans*. *PLoS Biology* 11: e1001653.

Nicotra, A. B., O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, et al. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15: 684–692.

Nikolov, L. A., P. Shushkov, B. Nevado, X. Gan, I. A. Al-Shehbaz, D. Filatov, C. D. Bailey, and M. Tsiantis. 2019. Resolving the backbone of the Brassicaceae phylogeny for investigating trait diversity. *New Phytologist* 222: 1638–1651.

Niu, X.-M., Y.-C. Xu, Z.-W. Li, Y.-T. Bian, X.-H. Hou, J.-F. Chen, Y.-P. Zou, et al. 2019. Transposable elements drive rapid phenotypic variation in *Capsella rubella*. *Proceedings of the National Academy of Sciences, USA* 116: 6908–6913.

Obeso, J. R. 2002. The costs of reproduction in plants. *New Phytologist* 155: 321–348.

O'Brien, A. M., C. N. Jack, M. L. Friesen, and M. E. Frederickson. 2021. Whose trait is it anyways? Coevolution of joint phenotypes and genetic architecture in mutualisms. *Proceedings of the Royal Society B* 288: 20202483.

O'Hara, N. B., J. S. Rest, and S. J. Franks. 2016. Increased susceptibility to fungal disease accompanies adaptation to drought in *Brassica rapa*. *Evolution* 70: 241–248.

Olson-Manning, C. F., C.-R. Lee, M. D. Rausher, and T. Mitchell-Olds. 2013. Evolution of flux control in the glucosinolate pathway in *Arabidopsis thaliana*. *Molecular Biology and Evolution* 30: 14–23.

Olson-Manning, C. F., C. F. Strock, and T. Mitchell-Olds. 2015. Flux control in a defense pathway in *Arabidopsis thaliana* is robust to environmental perturbations and controls variation in adaptive traits. *G3 Genes|Genomes|Genetics* 5: 2421–2427.

Opedal, Ø. H., E. Albertsen, and W. S. Armbruster. 2016. Evolutionary consequences of ecological factors: pollinator reliability predicts mating-system traits of a perennial plant. *Ecology Letters* 19: 1486–1495.

Palacio-López, K., B. Beckage, S. Scheiner, and J. Molofsky. 2015. The ubiquity of phenotypic plasticity in plants: a synthesis. *Ecology and Evolution* 5: 3389–3400.

Pecrix, Y., S. E. Staton, E. Sallet, C. Lelandais-Brière, S. Moreau, S. Carrère, T. Blein, et al. 2018. Whole-genome landscape of *Medicago truncatula* symbiotic genes. *Nature Plants* 4: 1017–1025.

Pennisi, E. 2010. Sowing the seeds for the ideal crop. *Science* 327: 802–803.

Petipas, R. H., A. W. Bowsher, C. S. Bekkering, C. N. Jack, E. E. McLachlan, R. A. White, B. S. Youngiger, et al. 2020. Interactive effects of microbes and nitrogen on *Panicum virgatum* root functional traits and patterns of phenotypic selection. *International Journal of Plant Sciences* 181: 20–32.

Pettengill, J. B., and D. A. Moeller. 2012. Tempo and mode of mating system evolution between incipient *Clarkia* species: temporal dynamics of mating system evolution. *Evolution* 66: 1210–1225.

Poveda, J., D. Eugui, and P. Velasco. 2020. Natural control of plant pathogens through glucosinolates: an effective strategy against fungi and oomycetes. *Phytochemistry Reviews* 19: 1045–1059.

Powers, J. M., H. M. Briggs, R. G. Dickson, X. Li, and D. R. Campbell. 2022a. Earlier snow melt and reduced summer precipitation alter floral traits important to pollination. *Global Change Biology* 28: 323–339.

Powers, J. M., A. K. Sakai, S. G. Weller, and D. R. Campbell. 2022b. Variation in floral volatiles across time, sexes, and populations of wind-pollinated *Schiedea globosa*. *American Journal of Botany* 109: 345–360.

Prasad, K. V., B. H. Song, C. Olson-Manning, J. T. Anderson, C. R. Lee, M. E. Schranz, A. J. Windsor, et al. 2012. A gain-of-function polymorphism controlling complex traits and fitness in nature. *Science* 337: 1081–1084.

Puzey, J. R., and E. M. Kramer. 2009. Identification of conserved *Aquilegia coerulea* microRNAs and their targets. *Gene* 448: 46–56.

Pyšek, P., and K. Prach. 1995. Invasion dynamics of *Impatiens glandulifera* — A century of spreading reconstructed. *Biological Conservation* 74: 41–48.

Qiao, J., X. Zhang, B. Chen, F. Huang, K. Xu, Q. Huang, Y. Huang, et al. 2020. Comparison of the cytoplastic genomes by resequencing: insights into the genetic diversity and the phylogeny of the agriculturally important genus *Brassica*. *BMC Genomics* 21: 480.

Rasmann, S., L. Pellissier, E. Defossez, H. Jactel, and G. Kunstler. 2014. Climate-driven change in plant–insect interactions along elevation gradients. *Functional Ecology* 28: 46–54.

Reed, T. E., R. S. Waples, D. E. Schindler, J. J. Hard, and M. T. Kinnison. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. *Proceedings of the Royal Society, B, Biological Sciences* 277: 3391–3400.

Rieseberg, L. H., S. J. E. Baird, and A. M. Desrochers. 1998. Patterns of mating in wild sunflower hybrid zones. *Evolution* 52: 713–726.

Rieseberg, L. H., O. Raymond, D. M. Rosenthal, Z. Lai, K. Livingstone, T. Nakazato, J. L. Durphy, et al. 2003. Major ecological transitions in wild sunflowers facilitated by hybridization. *Science* 301: 1211–1216.

Robinson, E. A., G. D. Ryan, and J. A. Newman. 2012. A meta-analytic review of the effects of elevated CO_2 on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist* 194: 321–336.

Roy, B. A. 1995. The breeding systems of six species of Arabis (Brassicaceae). *American Journal of Botany* 82: 869–877.

Roy, B. A., and L. H. Rieseberg. 1989. Evidence for apomixis in Arabis. *Journal of Heredity* 80: 506–508.

Rushworth, C. A., Y. Brandvain, and T. Mitchell-Olds. 2020. Identifying the fitness consequences of sex in complex natural environments. *Evolution Letters* 4: 516–529.

Rushworth, C. A., and T. Mitchell-Olds. 2021. The evolution of sex is tempered by costly hybridization in *Boechera* (rock cress). *Journal of Heredity* 112: 67–77.

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Rushworth, C. A., B. H. Song, C. R. Lee, and T. Mitchell-Olds. 2011. *Boechera*, a model system for ecological genomics. *Molecular Ecology* 20: 4843–4857.

Rushworth, C. A., M. D. Windham, R. A. Keith, and T. Mitchell-Olds. 2018. Ecological differentiation facilitates fine-scale coexistence of sexual and asexual *Boechera*. *American Journal of Botany* 105: 2051–2064.

Sakai, A. K., K. Karoly, and S. G. Weller. 1989. Inbreeding depression in *Schiedea globosa* and *S. salicaria* (Caryophyllaceae), subdioecious and gynodioecious Hawaiian species. *American Journal of Botany* 76: 437–444.

Sakai, A. K., and S. G. Weller. 1991. Ecological aspects of sex expression in subdioecious *Schiedea globosa* (Caryophyllaceae). *American Journal of Botany* 78: 1280–1288.

Salehin, M., B. Li, M. Tang, E. Katz, L. Song, J. R. Ecker, D. J. Kliebenstein, and M. Estelle. 2019. Auxin-sensitive Aux/IAA proteins mediate drought tolerance in *Arabidopsis* by regulating glucosinolate levels. *Nature Communications* 10: 4021.

Sampson, D. R. 1964. A one-locus self-incompatibility system in *Raphanus raphanistrum*. *Canadian Journal of Genetics and Cytology* 6: 435–445.

Scheiner, S. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24: 35–68.

Scheiner, S., and H. S. Callahan. 1999. Measuring natural selection on phenotypic plasticity. *Evolution* 53: 1704–1713.

Schilling, M. P., Z. Gompert, F.-W. Li, M. D. Windham, and P. G. Wolf. 2018. Admixture, evolution, and variation in reproductive isolation in the *Boechera puberula* clade. *BMC Evolutionary Biology* 18: 61.

Schlichting, C. D., and D. A. Levin. 1986. Phenotypic plasticity: an evolving plant character. *Biological Journal of the Linnean Society* 29: 37–47.

Schmitt, J., S. A. Dudley, and M. Pigliucci. 1999. Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. *The American Naturalist* 154: S43–S54.

Schranz, M. E., C. Dobes, M. A. Koch, and T. Mitchell-Olds. 2005. Sexual reproduction, hybridization, apomixis, and polyploidization in the genus *Boechera* (Brassicaceae). *American Journal of Botany* 92: 1797–1810.

Schwarz, D., A. J. Thompson, and H.-P. Kläring. 2014. Guidelines to use tomato in experiments with a controlled environment. *Frontiers in Plant Science* 5: 625.

Sharbel, T. F., M.-L. Voigt, J. M. Corral, G. Galla, J. Kumlehn, C. Klukas, F. Schreiber, et al. 2010. Apomictic and sexual ovules of *Boechera* display heterochronic global gene expression patterns. *Plant Cell* 22: 655–671.

Sicard, A., and M. Lenhard. 2018. Capsella. *Current Biology* 28: R920–R921.

Siemens, D. H., S. H. Garner, T. Mitchell-Olds, and R. M. Callaway. 2002. Cost of defense in the context of plant competition: *Brassica rapa* may grow and defend. *Ecology* 83: 505–517.

Simms, E. L., and M. D. Rausher. 1989. The evolution of resistance to herbivory in *Ipomoea purpurea*. II. *Natural selection by insects and costs of resistance. Evolution* 43: 573–585.

Sletvold, N., and J. Ågren. 2015. Climate-dependent costs of reproduction: Survival and fecundity costs decline with length of the growing season and summer temperature. *Ecology Letters* 18: 357–364.

Slotte, T., K. M. Hazzouri, J. A. Ågren, D. Koenig, F. Maumus, Y.-L. Guo, K. Steige, et al. 2013. The *Capsella rubella* genome and the genomic consequences of rapid mating system evolution. *Nature Genetics* 45: 831–835.

Song, B. H., M. Clauss, A. Pepper, and T. Mitchell-Olds. 2006. Geographic patterns of microsatellite variation in *Boechera stricta*, a close relative of *Arabidopsis*. *Molecular Ecology* 15: 357–369.

Song, B. H., and T. Mitchell-Olds. 2007. High genetic diversity and population differentiation in *Boechera fecunda*, a rare relative of *Arabidopsis*. *Mol Ecol* 16: 4079–4088.

St. Onge, K. R., T. Källman, T. Slotte, M. Lascoux, and A. E. Palmé. 2011. Contrasting demographic history and population structure in *Capsella rubella* and *Capsella grandiflora*, two closely related species with different mating systems: population structure and history in *Capsella*. *Molecular Ecology* 20: 3306–3320.

Stanton, M. L., A. A. Snow, S. N. Handel, and J. Bereczky. 1989. The impact of a flower-color polymorphism on mating patterns in experimental populations of wild radish (*Raphanus raphanistrum* L.). *Evolution* 43: 335–346.

Stanton, M., H. J. Young, N. C. Ellstrand, and J. M. Clegg. 1991. Consequences of floral variation for male and female reproduction in experimental populations of wild radish, *Raphanus sativus* L. *Evolution* 45: 268–280.

Stanton-Geddes, J., T. Paape, B. Epstein, R. Briskine, J. Yoder, J. Mudge, A. K. Bharti, et al. 2013. Candidate genes and genetic architecture of symbiotic and agronomic traits revealed by whole-genome, sequence-based association genetics in *Medicago truncatula*. *PLoS One* 8: e65688.

Stephan, W. 2019. Selective sweeps. *Genetics* 211: 5–13.

Stiling, P., and T. Cornelissen. 2007. How does elevated carbon dioxide (CO_2) affect plant–herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology* 13: 1823–1842.

Stratton, D. A., and C. C. Bennington. 1998. Fine-grained spatial and temporal variation in selection does not maintain genetic variation in *Erigeron annuus*. *Evolution* 52: 678–691.

Sultan, S. E., and H. G. Spencer. 2002. Metapopulation structure favors plasticity over local adaptation. *American Naturalist* 160: 271–283.

Szymański, J., S. Bocobza, S. Panda, P. Sonawane, P. D. Cárdenas, J. Lashbrooke, A. Kamble, et al. 2020. Analysis of wild tomato introgression lines elucidates the genetic basis of transcriptome and metabolome variation underlying fruit traits and pathogen response. *Nature Genetics* 52: 1111–1121.

Thairu, M. W., and J. Brunet. 2015. The role of pollinators in maintaining variation in flower colour in the Rocky Mountain columbine, *Aquilegia coerulea*. *Annals of Botany* 115: 971–979.

The Brassica rapa Genome Sequencing Project Consortium, X. Wang, H. Wang, J. Wang, R. Sun, J. Wu, S. Liu, et al. 2011. The genome of the mesopolyploid crop species *Brassica rapa*. *Nature Genetics* 43: 1035–1039.

Tiffin, P., and M. D. Rausher. 1999. Genetic constraints and selection acting on tolerance to herbivory in the common morning glory *Ipomoea purpurea*. *American Naturalist* 154: 700–716.

Timme, R. E., B. B. Simpson, and C. R. Linder. 2007. High-resolution phylogeny for *Helianthus* (Asteraceae) using the 18S-26S ribosomal DNA external transcribed spacer. *American Journal of Botany* 94: 16.

Tsuchimatsu, T., H. Kakui, M. Yamazaki, C. Marona, H. Tsutsui, A. Hedhly, D. Meng, et al. 2020. Adaptive reduction of male gamete number in the selfing plant *Arabidopsis thaliana*. *Nature Communications* 11: 2885.

Uller, T. 2008. Developmental plasticity and the evolution of parental effects. *Trends in Ecology & Evolution* 23: 432–438.

Underwood, C. J., K. Vijverberg, D. Rigola, S. Okamoto, C. Oplaat, R. H. M. O. den Camp, T. Radoeva, et al. 2022. A *PARTHENOGENESIS* allele from apomictic dandelion can induce egg cell division without fertilization in lettuce. *Nature Genetics* 54: 84–93.

Vaidya, P., A. McDurmon, E. Mattoon, M. Keefe, L. Carley, C.-R. Lee, R. Bingham, and J. T. Anderson. 2018. Ecological causes and consequences of flower color polymorphism in a self-pollinating plant (*Boechera stricta*). *New Phytologist* 218: 380–392.

Valladares, F., S. Matesanz, F. Guilhaumon, M. B. Araújo, L. Balaguer, M. Benito-Garzón, W. Cornwell, et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* 17: 1351–1364.

Van Etten, M. L., A. Kuester, S. Chang, and R. S. Baucom. 2016. Fitness costs of herbicide resistance across natural populations of the common morning glory, *Ipomoea purpurea*. *Evolution* 70: 2199–2210.

Van Etten, M., K. M. Lee, S.-M. Chang, and R. S. Baucom. 2020. Parallel and nonparallel genomic responses contribute to herbicide resistance in *Ipomoea purpurea*, a common agricultural weed. *PLoS Genetics* 16: e1008593.

Van Kleunen, M., J. P. M. Lenssen, M. Fischer, and H. De Kroon. 2007. Selection on phenotypic plasticity of morphological traits in response

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

to flooding and competition in the clonal shore plant *Ranunculus reptans*. *Journal of Evolutionary Biology* 20: 2126–2137.

Vanzela, A. L. L., P. M. Ruas, and M. A. Marin-Morales. 1997. Karyotype studies of some species of *Dalechampia* Plum. (Euphorbiaceae). *Botanical Journal of the Linnean Society* 125: 25–33.

Wadgymar, S. M., S. C. Daws, and J. T. Anderson. 2017. Integrating viability and fecundity selection to illuminate the adaptive nature of genetic clines. *Evolution Letters* 1: 26–39.

Wadgymar, S. M., R. M. Mactavish, and J. T. Anderson. 2018a. Transgenerational and within-generation plasticity in response to climate change: insights from a manipulative field experiment across an elevational gradient. *American Naturalist* 192: 698–714.

Wadgymar, S. M., J. E. Ogilvie, D. W. Inouye, A. E. Weis, and J. T. Anderson. 2018b. Phenological responses to multiple environmental drivers under climate change: insights from a long-term observational study and a manipulative field experiment. *New Phytologist* 218: 517–529.

Wagner, M. R., D. S. Lundberg, D. Coleman-Derr, S. G. Tringe, J. L. Dangl, and T. Mitchell-Olds. 2014. Natural soil microbes alter flowering phenology and the intensity of selection on flowering time in a wild *Arabidopsis* relative. *Ecology Letters* 17: 717–726.

Wagner, M. R., D. S. Lundberg, T. G. del Rio, S. G. Tringe, J. L. Dangl, and T. Mitchell-Olds. 2016. Host genotype and age shape the leaf and root microbiomes of a wild perennial plant. *Nature Communications* 7: 12151.

Wagner, M. R., and T. Mitchell-Olds. 2018. Plasticity of plant defense and its evolutionary implications in wild populations of *Boechera stricta*. *Evolution* 72: 1034–1049.

Walker, S. M., and J. K. Ward. 2018. Interactions between rising CO_2 and temperature drive accelerated flowering in model plants under changing conditions of the last century. *Oecologia* 187: 911–919.

Wallace, L. E., S. G. Weller, W. L. Wagner, A. K. Sakai, and M. Nepokroeff. 2009. Phylogeographic patterns and demographic history of *Schiedea globosa* (Caryophyllaceae) on the Hawaiian Islands. *American Journal of Botany* 96: 958–967.

Wang, B., J. P. Mojica, N. Perera, C. R. Lee, J. T. Lovell, A. Sharma, C. Adam, et al. 2019. Ancient polymorphisms contribute to genome-wide variation by long-term balancing selection and divergent sorting in *Boechera stricta*. *Genome Biology* 20: 126.

Warmke, H. E. 1954. Apomixis in *Panicum maximum*. *American Journal of Botany* 41: 5–11.

Watanabe, K., S. Stringer, O. Frei, M. Umićević Mirkov, C. de Leeuw, T. J. C. Polderman, S. van der Sluis, et al. 2019. A global overview of pleiotropy and genetic architecture in complex traits. *Nature Genetics* 51: 1339–1348.

WFO. 2022. World flora online. Published on the internet; website: www.worldfloraonline.org [accessed 11 August 2022].

Whitton, J., C. J. Sears, E. J. Baack, and S. P. Otto. 2008. The dynamic nature of apomixis in the angiosperms. *International Journal of Plant Sciences* 169: 169–182.

Wickland, D. P., and Y. Hanzawa. 2015. The *FLOWERING LOCUS T/TERMINAL FLOWER 1* gene family: functional evolution and molecular mechanisms. *Molecular Plant* 8: 983–997.

Wilczek, A. M., M. D. Cooper, T. M. Korves, and J. Schmitt. 2014. Lagging adaptation to warming climate in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* 111: 7906–7913.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687–690.

Willis, S. G., and P. E. Hulme. 2002. Does temperature limit the invasion of *Impatiens glandulifera* and *Heracleum mantegazzianum* in the UK?: Climate and non-indigenous plant performance. *Functional Ecology* 16: 530–539.

Wolfe, L. M., J. A. Elzinga, and A. Biere. 2004. Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*: decreased resistance in an invasive plant. *Ecology Letters* 7: 813–820.

Wu, C. A., D. B. Lowry, L. I. Nutter, and J. H. Willis. 2010. Natural variation for drought-response traits in the *Mimulus guttatus* species complex. *Oecologia* 162: 23–33.

Yan, W., B. Wang, E. Chan, and T. Mitchell-Olds. 2021. Genetic architecture and adaptation of flowering time among environments. *New Phytologist* 230: 1214–1227.

Yang, L., H.-N. Wang, X.-H. Hou, Y.-P. Zou, T.-S. Han, X.-M. Niu, J. Zhang, et al. 2018. Parallel evolution of common allelic variants confers flowering diversity in *Capsella rubella*. *The Plant Cell* 30: 1322–1336.

Yoder, J. B., J. Stanton-Geddes, P. Zhou, R. Briskine, N. D. Young, and P. Tiffin. 2014. Genomic signature of adaptation to climate in *Medicago truncatula*. *Genetics* 196: 1263–1275.

Yu, H.-J., S. Baek, Y.-J. Lee, A. Cho, and J.-H. Mun. 2019. The radish genome database (RadishGD): an integrated information resource for radish genomics. *Database* 2019: baz009. https://doi.org/10.1093/database/baz009

Yu, X., H. Wang, W. Zhong, J. Bai, P. Liu, and Y. He. 2013. QTL Mapping of leafy heads by genome resequencing in the RIL population of *Brassica rapa*. *PLoS One* 8: e76059.

Zhang, H., T. Mitchell-Olds, I. Mujacic, and B.-H. Song. 2020. De novo genome assembly, *annotation, and SNP identification of an endangered rockcress, Boechera fecunda*. *Frontiers in Ecology and Evolution* 8: 550936.

How to cite this article: Rushworth, C. A., M. R. Wagner, T. Mitchell-Olds, and J. T. Anderson. 2022. The Boechera model system for evolutionary ecology. *American Journal of Botany* 109(11): 1–23 https://doi.org/10.1002/ajb2.16090

15372197, 0, Downloaded from https://bsapubs.onlinelibrary.wiley.com/doi/10.1002/ajb2.16090 by Utah State University, Wiley Online Library on [14/11/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License