Genetic adaptation to climate change in wild populations: a systematic literature review identifies opportunities to strengthen our evidence base

Natalie E. van Dis[1,2,3]

ORCID ID: 0000-0002-9934-6751

[1] Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB, Wageningen, The Netherlands

[2] Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC, Groningen, The Netherlands

[3] Organismal and Evolutionary Biology, University of Helsinki, P.O. Box 4, 00014 Helsinki, Finland

✉ natalie.vandis@helsinki.fi

Keywords: global warming, microevolution, rapid adaptation, genetic change, natural selection, evolutionary rescue

Abstract

To understand to what extent evolution can contribute to bending the curve of ongoing biodiversity losses, we urgently need to characterize the adaptive potential of populations. This systematic literature review comprehensively gathers existing examples of genetic adaptation to climate change to (1) guide efforts to assess genetic adaptation to climate change in a wider variety of species and ecosystems, and (2) allow the field to capitalize on these existing examples to advance our knowledge on the drivers and constraints underlying climate change adaptation. I identified 51 case studies of 49 species for which genetic change over time in response to climate change has been strongly inferred in wild populations. I furthermore assessed the strength of evidence for each study on five criteria that together robustly demonstrate that these genetic changes are adaptive and in response to climate change: in addition to (1) demonstrating genetic change over time, I determined whether strong inference methods were used to show that (2) a phenotypic change over time occurred, (3) the fitness of the phenotype depends on a climatic variable, (4) climate change-induced selection occurred across generations, and (5) the relative contribution of adaptive and neutral evolutionary processes was assessed. While taxonomic and ecosystem representation need to be improved in the future, patterns emerging from the resulting overview indicate that genetic responses to climate change are happening in many of the species tested and are often population specific, with selection affecting populations both directly and indirectly. However, to further validate and elucidate the frequency of genetic adaptation under climate change and its underlying drivers and constraints, more studies are needed. I identify three key opportunities for the field to strengthen and supplement our evidence base: (1) harness the power of temporal genomics approaches to gain important information about the process and rate of evolution and to allow for assessing genetic change in species and populations that might otherwise be hard to sample, (2) perform follow-up phenotypic characterization and experimentation for 44 of the existing and an additional 84 suggestive examples of genetic adaptation to climate change such that they can contribute to improving the prediction of population responses, and (3) improve spatial and temporal replication to allow for the exciting opportunity to start empirically testing drivers and constraints that determine the likelihood and rate of genetic adaptation to climate change.

1. Introduction

Climate change is exerting strong selection pressures on wild populations, with biodiversity losses starting to accumulate (IPCC, 2022). In the long run, only microevolution will allow populations to persist, as the pace and magnitude of environmental change cause populations to experience novel conditions outside their phenotypic plasticity spectrum, whether in their home range or after range shifting (Gonzalez et al., 2013; Visser, 2008). For effective conservation, we thus need to know what determines a population's evolutionary potential to be able to predict species' responses to climate change (Eizaguirre & Baltazar-Soares, 2014; Urban et al., 2016). A large variety of approaches is used to predict population adaptive potential under future climate change, including space-for-time substitutions and experimental assessments – both in the lab and in the field [see for recent reviews of the field (Lovell et al., 2023; Urban et al., 2024)]. However, to understand to what extent these approaches can accurately predict genetic adaptation to climate change, we also need to directly observe genetic adaptation in natural populations and use these case studies to validate and further elucidate the drivers and constraints of rapid adaptation (Franks & Hoffmann, 2012; Lovell et al., 2023; Merilä & Hendry, 2014).

Genetic adaptation is a ubiquitous process in nature and has frequently been observed to occur rapidly – over just a few generations – in response to both natural and human-induced selection pressures (Carroll et al., 2007; Cook & Saccheri, 2013; Czorlich et al., 2022; Grant & Grant, 2003; Norris et al., 2015). Ultimately, genetic evidence over a period of multiple generations is needed to convincingly show an evolutionary response to selection. Such temporal data allow for the direct observation of adaptation in real-time, which is needed to confidently establish when the genetic change took place (Hansen et al., 2012; Merilä & Hendry, 2014). Moreover, such temporal data allow for pinpointing which environmental drivers are likely to have caused the observed genetic change, especially when combined with in-depth knowledge about the phenotype under selection (Franks & Hoffmann, 2012; Merilä & Hendry, 2014; Urban et al., 2024). In addition to phenotypic characterization, a powerful method to investigate microevolution is population genomic analysis of temporal samples, allowing for the assessment of population evolutionary history to help distinguish between different evolutionary processes that lead to genetic change over time [e.g. response to selection, gene flow, genetic drift (Barghi et al., 2020; Clark et al., 2023)].

Importantly, while sampling a population at two timepoints (i.e. before and after environmental change) might already allow for directly observing genetic change, a key problem with just two time points is that it can lead to erroneous conclusions. Not only adaptation, but also drift and gene flow can result in differences in allele frequency over time, causing cumulative changes in the genomic composition of a population. Moreover, sampling more than two timepoints is needed to be able to confirm that the population is adapting to climate change rather than individual climate fluctuations [i.e. showing a consistent and directional genetic change over time in response to climate change (Endler, 1986; Urban et al., 2024)]. Similarly, evidence for climate being the causal driver for the observed genetic adaptation is greatly improved when the same response is observed in replicate populations (Compagnoni et al., 2024; Endler, 1986). Comparing replicate populations on aspects such as selection strength and initial levels of phenotypic/genetic variation would furthermore provide important insights into what determines a population’s adaptive potential under climate change, since responses to climate change can differ substantially across a species' range [e.g. (Bailey et al., 2022; Dunn et al., 2023; Jantzen & Visser, 2023)].

To improve our ability to predict evolutionary rescue under climate change, there are calls to initiate long-term monitoring programs to gain the temporal data needed to assess genetic adaptation to climate change in a wider variety of species and ecosystems [e.g. (Clark et al., 2023; Jensen & Leigh, 2022; Urban et al., 2024)]. To guide these efforts, we need a comprehensive overview of which species and populations have been assessed for genetic adaptation to climate change to date. Moreover, as temporal data take time to accumulate, it would be highly beneficial to meanwhile capitalise on existing examples of genetic adaptation in natural populations to advance our knowledge on the drivers and constraints underlying climate change adaptation. However, the last systematic literature review on wild populations genetically adapting to climate change was performed more than a decade ago [(Merilä & Hendry, 2014) and references therein].

The purpose of the current paper is to update the (Merilä & Hendry, 2014) review and comprehensively gather studies showing direct evidence of wild populations undergoing genetic adaptation in response to climate change selection. Due to this specific focus, the overview presented here is thus limited to studies that sampled at least two time points in wild populations of native species [for recent insights on rapid genetic adaptation from invasive species, see (Kołodziejczyk et al., 2025)]. I start by outlining criteria for demonstrating genetic adaptation to climate change [following (Franks & Hoffmann, 2012; Hansen et al., 2012; Merilä & Hendry, 2014)], and then summarize and assess the evidence for microevolution in each identified study. I will discuss how the field has progressed in the last decade and will pay particular attention to studies that collected data for more than two timepoints, for multiple populations, and studies that collected genomic data, as such studies provide highly needed opportunities to elucidate drivers and constraints that determine the likelihood and rate of adaptation to climate change in wild populations. This review will allow the field to better utilize existing examples of genetic adaptation to climate change to improve the predictability of genetic adaptation to climate change.

2. Methods

2.1 Criteria for demonstrating genetic adaptation driven by climate change

To assess the evidence for genetic adaptation to climate change selection, I built on similar reviews performed in the previous decade and the assessment criteria outlined therein (Franks & Hoffmann, 2012; Hansen et al., 2012; Merilä & Hendry, 2014). I define five criteria that studies should meet to demonstrate that a wild population is genetically adapting to climate change (Table 1), in the following order of importance:

Foremost, studies need to test whether the population shows genetic change over time (criterium 1). To assess whether this observed genetic change is indeed an adaptation to climate change, it is furthermore necessary to establish the phenotype under climate change selection. Thus, studies need to assess which phenotype has changed in mean trait value over time (criterium 2) and demonstrate that the observed change is adaptive and driven by climate change by providing evidence that (a) the fitness of that phenotype depends on a climatic variable (criterium 3), and (b) that climate change selection – whether direct or indirect – has actually occurred in the population (criterium 4; as opposed to genetic adaptation occurring solely in response to other selection pressures). In this regard, an environmental assessment is important to differentiate natural climate fluctuations from climate change, by showing that the climate selection a population is subjected to is indeed directional (e.g. long-term increases in mean temperature, increased frequency of droughts etc.). Finally, studies need to distinguish between different evolutionary processes underlying the observed population genetic change (i.e. response to selection, gene flow, spatial sorting and genetic drift; criterium 5). While in essence, each process can lead to adaptive genetic change in the population, their relative contribution would lead to different conclusions when using these findings to assess population adaptative potential under climate change. For example, identifying the sources of genetic variation that are most important for rapid adaptation to climate change (e.g. whether gene flow or standing genetic variation plays a more important role) will improve the assessment of population vulnerability (Waldvogel et al., 2020).

To also assess the strength of evidence for genetic adaptation to climate change selection, I considered the level of replication (both temporal and spatial, see introduction), as well as whether studies used strong inference methods [following (Hansen et al., 2012; Merilä & Hendry, 2014)]. Table 1 lists the five assessment criteria including the methods that provide strong evidence for each criterium [see for an in-depth discussion of why these methods are strong (Merilä & Hendry, 2014)]. To illustrate, consider the following example: (Bonnet et al., 2019) used yearly long-term observations of individually marked wild red deer and their relatedness to statistically estimate the heritability of parturition date and quantify the genetic contribution (strong evidence criterium 1: animal models and many timepoints, see Table 1) underlying progressive advancement of parturition date observed in the population (strong evidence criterium 2: repeated field observations of the mean phenotype and many timepoints). Evidence that this change is adaptive and driven by climate change comes from the fact that the onset of the plant growing season (i.e. the red deer's food source) also advanced over time due to a significant increase in the number of growing degree days [directional change in climate variable, (Moyes et al., 2011)] and females with earlier parturition dates had higher lifetime breeding success (strong evidence criterium 4: selection estimates and many timepoints). However, aside from the fact that fitness increased with earlier parturition date for a higher number of growing degree days, the fitness of the phenotype was not experimentally linked to this climatic variable (suggestive evidence criterium 3: correlational not causal). Finally, due to yearly monitoring of the population, the authors could statistically estimate the effect of gene flow and drift to show that these processes had little effect on the observed genetic change (strong evidence criterium 5: animal models and many timepoints).

Table 1. Criteria and strong methods for demonstrating genetic adaptation driven by climate change. Criteria build on previous reviews by (Franks & Hoffmann, 2012; Hansen et al., 2012; Merilä & Hendry, 2014)] and are presented in order of importance. Strength of evidence for each criterium was assessed by determining whether the listed strong methods were used for inference (Table S2; see main text for an example).

Criterium (1)	Demonstrate that the population shows genetic change over time, ideally linked to the phenotype under selection (see criteria 2-4 below).
Strong methods:	• molecular genetic approaches • trait known to be fully genetically determined • repeated common-garden experiments combined with evidence for trait heritability (i.e. accounting for maternal and storage effects) • animal models [i.e. mixed models incorporating multigenerational / pedigree information to statistically estimate genetic parameters (Kruuk, 2004)]
Criterium (2)	Establish that the mean phenotype of a particular trait has changed in the population over time.
Strong methods:	• repeated field observations • repeated common-garden experiments
Criterium (3)	Provide evidence that the fitness of the phenotype depends on a climatic variable.
Strong methods:	• reciprocal transplants • experimental studies
Criterium (4)	Show that directional climate change-induced selection on the trait has occurred in the population across generations.
Strong methods:	• phenotypic/genotypic selection estimates • experimental evolution
Criterium (5)	Assess the relative contribution of adaptive and neutral evolutionary processes (i.e. response to selection, gene flow, spatial sorting, genetic drift).
Strong methods:	• molecular genetic approaches • animal models • absolute population tracking (e.g. in a closed lake)

2.2 Systematic literature review

To gather examples of genetic adaptation to climate change, I performed a systematic literature search on the Web of Science (WoS) using a combination of different key words [('climate change' OR 'climate warming' OR 'global warming') + ('evolution*' OR 'microevolution') + ('rapid adaptation' OR 'rapid shift' OR ‘rapid change’) + 'genetic', 1245 records, accessed on 2025-02-26]. I first performed a selection round, reading all titles and abstracts, only selecting records that tested for genetic change over time in wild populations in the context of climate change (see Table S1a). I selected 46 records to read in-depth, summarizing and assessing whether the five criteria outlined in the previous section were met (if necessary, reading additional papers on the study system when these came up in the search or were cited as evidence, Table S2), thus highlighting species with strong evidence of genetic adaptation in response to climate change. I also determined whether the trait under study is plastic (i.e. evidence presented that the expression of the trait depends on a climatic variable), how many timepoints each study sampled, for how many populations, whether genomic data was collected, and whether the underlying data is openly available (Table S2). To ensure I did not miss any recent papers, I did an additional WoS search for papers published in the last three years, using a broader set of key words [('climate change' OR 'climate warming' OR 'global warming' OR 'climat* selection') + 'evolution' + ('adaptation' OR 'selection'), 779 records in WoS categories ‘Ecology’ and ‘Evolutionary Biology’, accessed on 2025-02-26], leading to an additional 9 records selected for assessment (Table S2). Finally, I assessed an additional 56 papers that came to my attention while selecting and assessing the WoS records [e.g. examples identified in previous literature reviews (Merilä & Hendry, 2014 and references therein; Scheffers et al., 2016) and examples or evidence cited by assessed studies, Table S2].

3. Examples of genetic adaptation to climate change

3.1 Overview and emerging patterns

Taxonomic and ecosystem representation

The systematic literature review identified 43 empirical examples of species with direct evidence of wild populations undergoing genetic adaptation in response to climate change selection (Table 2, from 58 published papers). Moreover, several studies were identified that tested for genetic adaptation to climate change, but that did not find evidence of genetic change over time (Table 3, N=8 species from 15 published papers). Together, these 51 studies encompassed 49 species in nine higher taxa, with the fast majority being plants (Fig.1; genetic change: 19 plants, 7 insects, 4 birds, 3 crustaceans, 3 mammals, 2 fish, 2 molluscs, 2 algae, and 1 reptile; no genetic change: 2 birds, 3 mammals, 2 plants, 1 fish). Fungi, amphibians, microbes and protists are not yet in this list and thus represent important target taxa for long-term monitoring programs to improve taxonomic and ecosystem representation in the assessment of genetic adaptation to climate change [e.g. (Clark et al., 2023; Cocciardi et al., 2024; Urban et al., 2024)]. There is also ample scope to diversify sample locations, as most studies to date focused on temperate regions in Europe and North America (Fig.1), investigating the terrestrial realm (N=41 species). To increase ecosystem representation in the future, more studies on fresh-water species (currently N=4), marine species (currently N=4), tropical species (currently N=1), and polar species (currently none) are needed.

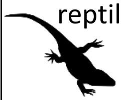
Table 2. Examples of genetic adaptation driven by climate change. The systematic literature review identified 43 examples of species, from nine higher taxa, with wild populations genetically adapting to climate change over time. For each species, I assessed whether strong evidence was provided for the five criteria that demonstrate that a wild population is genetically adapting to climate change (Table 1). For each study system, it is also noted which trait was studied; whether expression of the trait depends on a climatic variable (i.e. climate plasticity); how many timepoints were studied; how many populations; whether genomic data has been collected; and whether the underlying data is openly available (see Fig.2A for a summary of the available evidence). Studies highlighted in grey provide strong evidence for each of the first four criteria [light grey] or all five assessment criteria [dark grey]. Cells highlighted in green note studies with at least three timepoints and/or populations.

‘y’ = yes, ‘n’ = no, ‘p’ = partly/processed only; capital ‘**Y**’ in bold = strong inference methods used (see Table 1); small ‘*y*’ in italics = no strong inference methods used; P=plastic, NP=not plastic, ?=no evidence provided.

Taxa	Species	Trait	Climate plastic trait?	# Timepoints	# Populations	(1) Genetic change?	(2) Temporal change in phenotype?	(3) Fitness climate dependent?	(4) Climate change selection?	(5) Assessed which evolutionary processes?	Genomic data collected?	Data available?	Refs
alga 	*spring bloom dinoflagellate *Apocalathium malmogiense*	Physiology	P	2	1	**Y**	**Y**	n	*y* 🌡	n		Y	Hinners et al., 2017
	*cold-water kelp *Laminaria digitata*	(allele frequency)	?	2	3	**Y**	n	n	*y* 🌡	**Y**	Y	Y	Reynes et al., 2024
bird 	black cap (*Sylvia atricapilla*)	Phenology	?	13	1	**Y**	**Y**	n	*y* 🌡	n		n	Pulido & Berthold, 2010
	*collared flycatcher (*Ficedula albicollis*)	Coloration	P	34	1	**Y**	**Y**	*y*	**Y** 🌡	n		Y	Evans & Gustafsson, 2017
	*southwestern willow flycatcher (*Empidonax traillii extimus*)	(allele frequency)	?	2	1	**Y**	n	n	*y* 🌡 🌧	**Y**	Y	Y	Turbek et al., 2023
	tawny owl (*Strix aluco*)	Coloration	NP	28	1	**Y**	**Y**	*y*	**Y** 🌡 🌨	**Y**		n	Karell et al., 2011
crustacean	*water flea *Daphnia galeata*	Growth; Thermal tolerance	P	2	1	**Y**	*y*	n	*y* 🌡	**Y**		n	Henning-Lucass et al., 2016

	*water flea *Daphnia magna*	Thermal tolerance	?	2	1	**Y**	**Y**	**Y**	**Y** 🌡	**Y**	Y	*p*	Geerts et al., 2015; Jansen et al., 2017
	*water flea *Daphnia pulicaria*	Thermal tolerance	?	3	1	**Y**	**Y**	**Y**	*y* 🌡	n		Y	Yousey et al., 2018
fish 	pink salmon (*Oncorhynchus gorbuscha*)	Phenology	?	8	2	**Y**	**Y**	*y*	*y* 🌡	n		Y	Kovach et al., 2012
	*threespine stickleback (*Gasterosteus aculeatus*)	Morphology	NP	4	25	**Y**	**Y**	*y*	*y* 🌡 🌵	n		Y	Des Roches et al., 2020
insect 	*Drosophila melanogaster*	(allele frequency)	?	2	34	**Y**	n	*y*	*y* 🌡	n		n	Umina et al., 2005
	Drosophila robusta	(allele frequency)	?	18	22	**Y**	n	*y*	*y* 🌡	*y*		*p*	Etges & Levitan, 2008
	Drosophila subobscura	(allele frequency)	?	9	43	**Y**	n	**Y**	*y* 🌡 ⚡	*y*		*p*	Balanya et al., 2006; Rodríguez-Trelles et al., 2013; Rodríguez-Trelles & Rodríguez, 1998; Zivanovic et al., 2015, 2019
	pitcher-plant mosquito (*Wyeomyia smithii*)	Phenology	?	2	>=8	**Y**	*y*	*y*	*y* 🌡	n		n	Bradshaw & Holzapfel, 2001
	two-spot ladybird (*Adalia bipunctata*)	Coloration	NP	5	1	**Y**	**Y**	**Y**	*y* 🌡	n		n	Brakefield & De Jong, 2011
	*winter moth (*Operophtera brumata*)	Phenology	P	16	3	**Y**	**Y**	**Y**	**Y** 🌡	n		n	van Asch et al., 2013
	*yellow dung fly (*Scathophaga stercoraria*)	Body size	P	12	1	**Y**	**Y**	*y*	*y* 🌡	n		Y	Blanckenhorn, 2015
mammal 	*red deer (*Cervus elaphus*)	Phenology	P	45	1	**Y**	**Y**	*y*	**Y** 🌡	**Y**		Y	Bonnet et al., 2019; Moyes et al., 2011
	red squirrel (*Tamiasciurus hudsonicus*)	Phenology	?	13	1	**Y**	**Y**	n	*y* 🌡	n		n	Réale et al., 2003
	*snow vole (*Chionomys nivalis*)	Body size	P	9	1	**Y**	**Y**	*y*	**Y** 🌡 🌨	**Y**		Y	Bonnet et al., 2017
mollusc 	land snail *Cepaea hortensis*	Coloration	NP	3	>=2	**Y**	**Y**	**Y**	*y* 🌡	n		n	Cameron & Pokryszko, 2008; Cowie & Jones, 1998
	land snail *Cepaea nemoralis*	Coloration	NP	6	>=9	**Y**	**Y**	**Y**	*y* 🌡	*y*		*p*	Cameron & Cook, 2013; Cowie & Jones, 1998; Ożgo & Schilthuizen, 2012

plant 🌿	**Arabidopsis thaliana*	Phenology	P	2	1	**Y**	**Y**	*y*	*y* 🌡	**Y**	Y	Y	Frachon et al., 2017 *but see Table 3*
	**Clarkia xantiana*	Phenology	?	3	2	**Y**	**Y**	**Y**	**Y** 🌳	n		Y	Benning et al., 2023
	**Clinopodium vulgare*	Growth; Phenology	P	2	1	**Y**	**Y**	**Y**	*y* 🌳	**Y**		Y	Karitter et al., 2024; Rauschkolb et al., 2022
	*cornflower (*Centaurea cyanus*)	Phenology	?	2	1	**Y**	**Y**	n	*y* 🌡	**Y**		n	Thomann et al., 2015
	*cutleaf monkeyflower (*Mimulus laciniatus*)	Phenology	?	2	9	**Y**	**Y**	**Y**	*y* 🌳	n		Y	Dickman et al., 2019
	**Cyanus segetum*	Growth; Phenology	?	2	3	**Y**	**Y**	**Y**	*y* 🌡	**Y**		Y	Valencia-Montoya et al., 2021
	*European beech (*Fagus sylvatica*)	(allele frequency)	?	4	1	**Y**	n	*y*	*y* 🌡	*y*	Y	n	Jump et al., 2006
	field mustard (*Brassica rapa*)	Phenology; Physiology	P	4	2	**Y**	**Y**	**Y**	**Y** 🌳	**Y**	Y	*p*	Franks, 2011; Franks et al., 2007, 2016; Franks & Weis, 2008; Hamann et al., 2018, 2021; Welt et al., 2015
	**Leontodon hispidus*	Growth; Phenology	P	2	1	**Y**	**Y**	**Y**	*y* 🌳	**Y**		Y	Karitter et al., 2024; Rauschkolb et al., 2022
	**Matthiola tricuspidata*	Growth; Phenology	P	2	1	**Y**	**Y**	**Y**	*y* 🌳	**Y**		Y	Rauschkolb et al., 2022
	**Plantago crassifolia*	Physiology	P	2	1	**Y**	**Y**	**Y**	*y* 🌳	**Y**		Y	Rauschkolb et al., 2022
	*San Francisco collinsia (*Collinsia multicolor*)	Phenology; Physiology	P	2	3	**Y**	*y*	*y*	*y* 🌳	n		n	Spurlin & Lambrecht, 2024
	*scarlet monkeyflower (*Mimulus cardinalis*)	Phenology; Physiology	P	7	3	**Y**	*y*	n	*y* 🌳	n		Y	Anstett et al., 2021; Branch et al., 2024 *but see Table 3*
	**Schoenoplectus americanus*	Growth	P	2	2	**Y**	**Y**	n	*y* 📈 🌊	**Y**		*p*	Vahsen et al., 2023
	*true babystars (*Leptosiphon bicolor*)	Growth; Phenology	P	2	3	**Y**	**Y**	n	*y* 🌳	n		Y	Lambrecht et al., 2020
	wild emmer wheat (*Triticum dicoccoides*)	Phenology	P	2	10	**Y**	**Y**	*y*	*y* 🌡 🌳	n		Y	Nevo et al., 2012
	*wild oat (*Avena fatua*)	Growth	P	2	1	**Y**	*y*	*y*	*y* 📈	n		n	Ziska, 2017

	*wild pansy (*Viola arvensis*)	Phenology	?	2	1	**Y**	**Y**	n	*y* 🌡	n		Y	Cheptou et al., 2022
	wild Thyme (*Thymus vulgaris*)	Physiology	NP	2	24	**Y**	**Y**	**Y**	**Y** 🌡	*y*		n	Thompson et al., 2013
reptile 	*green anole lizard (*Anolis carolinensis*)	Thermal tolerance	?	2	5	**Y**	**Y**	*y*	*y* 🌡 ⚡	n	Y	Y	Campbell-Staton et al., 2017

Notes on table legend:

- * = Study systems newly identified compared to the last systematic literature review on natural populations genetically adapting to climate change, performed more than a decade ago [N=29 new since (Merilä & Hendry, 2014) and references therein].
- The type of climate change selection pressure investigated is indicated with icons: 🌡=temperature; 🌧 /🌨=precipitation [rain/snow]; 🏜= drought; 📈=CO2; 🌊=inundation & salinity; ⚡=extreme event
- See Table S2 for a summary of the evidence for each underlying paper assessed per species (cited here under Refs).
- Taxa pictures were freely available in the public domain and obtained via https://www.phylopic.org/.

Table 3. Examples showing *no* genetic adaptation in response to climate change. The systematic literature review identified 8 examples of species with wild populations that were tested for genetic adaptation to climate change, but where no genetic change was found. The table legend used is the same as Table 2 (see above).

Taxa	Species	Trait	Climate plastic trait?	# Timepoints	# Populations	(1) Genetic change?	(2) Temporal change in phenotype?	(3) Fitness climate dependent?	(4) Climate change selection?	(5) Assessed which evolutionary processes?	Genomic data collected?	Data available?	Refs
bird 	*blue tit (*Cyanistes caeruleus*)	Phenology	P	44	1	**Y**	**Y**	*y*	**Y** 🌡	n		Y	Biquet et al., 2022; Bonamour et al., 2019
	great tit (*Parus major*)	Phenology	P	50	2	**Y**	**Y**	*y*	**Y** 🌡	n		Y	Charmantier et al., 2008; Gienapp et al., 2006; Ramakers et al., 2019; Simmonds et al., 2020
fish 	*Atlantic salmon (*Salmo salar L.*)	Growth	P	25	1	**Y**	**Y**	*y*	*y* 🌡	**Y**	Y	Y	Besnier et al., 2024; Harvey et al., 2022
mammal 	*lodgepole chipmunk (*Tamias speciosus*)	(allele frequency)	?	2	1	**Y**	**Y**	n	*y* 🌡	**Y**	Y	Y	Bi et al., 2019
	Soay sheep (*Ovis aries*)	Body size	P	21	1	**Y**	**Y**	*y*	*y* 🌡?	**Y**		n	Ozgul et al., 2009
	yellow-bellied marmots (*Marmota flaviventer*)	Body size; Phenology	P	33	1	**Y**	**Y**	*y*	**Y** 🌡🌨	n		p	Inouye et al., 2000; Ozgul et al., 2010; St. Lawrence et al., 2023
plant 	**Arabidopsis thaliana*	Phenology	?	2	4	**Y**	*y*	*y*	*y* 🌡🌧	*y*		Y	Gómez et al., 2018 *but see Table 2*
	*scarlet monkeyflower (*Mimulus cardinalis*)	Phenology; Thermal tolerance	P	2	6	**Y**	**Y**	*y*	*y* 🌡🏜	n		Y	Vtipil & Sheth, 2020; Wooliver et al., 2020 *but see Table 2*

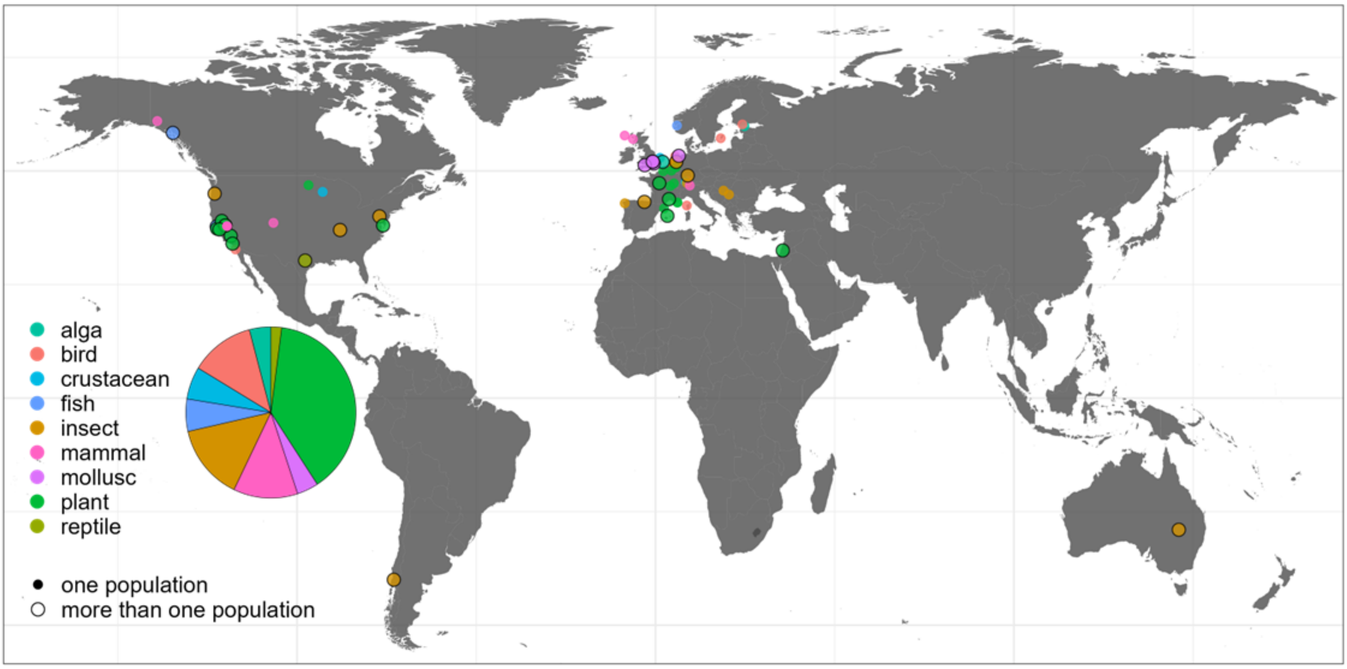


Figure 1. Taxonomic and ecosystem representation of climate change genetic adaptation examples. The world map gives the spatial distribution of the 72 published papers encompassing 49 species with wild populations tested for genetic adaption to climate change over time. Depicted are the locations of the studied species (latitude/longitude in decimals), with one point per published paper, coloured by taxa. The pie chart shows the proportion of species studied per taxon (genetic change: 19 plants, 7 insects, 4 birds, 3 crustaceans, 3 mammals, 2 fish, 2 molluscs, 2 algae, and 1 reptile [Table 2]; no genetic change: 2 birds, 3 mammals, 2 plants, 1 fish [Table 3]).

NB: If more than one population was studied (point with black outline), I included the midpoint of the studied populations/cline. Duplicate papers are not depicted (i.e. papers studying the exact same populations), while for one paper, three points were included: one for each cline studied on three different continents (total points depicted: N=60). Map base source: R Package "maps" v.3.4.2. Shapefile: Natural Earth https://www.naturalearthdata.com/about/terms-of-use/.

Frequency of genetic change vs. plasticity

Together, the 51 identified case studies cautiously suggest that in many cases where populations are tested for genetic change over time (criterium 1), genetic change is found. Phenotypes that have genetically changed over time included phenology (N=20), growth (e.g. growth rate, reproductive biomass, plant size, N=8), physiology (e.g. water-use efficiency, stem diameter, N=6), coloration (N=5), thermal tolerance (N=4), body size (N=2), and morphology (N=1, Table 2); with some studies yet to identify the phenotype under selection from climate change, having only sampled molecular genetic data (i.e. no evidence for criterium 2, N=6, Table 2). Phenotypes that were not found to have genetically changed included phenology (N=5), body size (N=2), thermal tolerance (N=1) and growth (i.e. age at maturity, N=1, Table 3). Note that many of the latter studies did find phenotypic change, thus highlighting the significant contribution of plastic responses in population responses to climate change. Indeed, of the studies that tested for phenotypic change, many phenotypes were found to also plastically respond to climate variables (N=25 studies, Table 2 and 3), with the few nonplastic phenotypes all involving genetically determined colour morphs or ecotypes (N=6, Table 2). Interestingly, studies that found genetic change in plastic traits mostly found changes over time in the mean phenotypic trait value of populations, with studies that explicitly tested for genetic change in plasticity often finding little or no evolution of phenotypic plasticity (i.e. little change in the magnitude of the phenotype response to climatic variables, e.g. insect *Operophtera brumata*, crustacean *Daphnia magna*, plants *Clinopodium vulgare*, *Brassica rapa*, *Leptosiphon bicolor*; see Table S2). However, for a large portion of the studies, plasticity of the phenotype under climate selection remains unknown (N=20, Table 2 and 3), needing follow-up studies to investigate the relative contribution of plasticity and genetic change in determining population responses to climate change (Charmantier & Gienapp, 2014; Merilä & Hendry, 2014). It is important to note that, while the studies that tested but did not find genetic change in wild populations under climate change were fewer in number, this result could still represent an artificial bias rather than a real result – e.g. as a consequence of the fact that null results tend to get published less (Jennions & Møller, 2002; Yang et al., 2023) and/or these studies having a different narrative than affirmative studies, thus making them less likely to be included by the used search terms. Efforts to test for genetic change over time in more species and populations, and taking extra care to also publish null results, are crucial to further validate the frequency of genetic adaptation in response to climate change.

Selection pressures exerted by climate change

Climate change selection on populations was most often reported to be through mean temperature (N=38), followed by precipitation (N=18, with the majority specifically dealing with periods of drought [N=13 of which N=12 in plants]), extreme temperature events (N=2), CO2 levels (N=2), and/or inundation and change in salinity (N=1, Table 2 and 3). While for most species, climate change selection seems to be related to temperature (N=31 species) or precipitation (N=17 species) or both (N=8 species), studies that performed in-depth phenotypic characterization (i.e. with evidence for criteria 2 and 3, Table 2 and 3) indicate that while climate change often directly impacts fitness (e.g. crustacean *Daphnia* species, insect *Adalia bipunctata*, mollusc *Cepaea hortensis*, reptile *Anolis carolinensis*, and drought tolerance in many plant species), selection also frequently operates indirectly through changing species interactions – such as phenological matches between consumer and their food source or sexual selection (e.g. insects *Wyeomyia smithii*, *Scathophaga stercoraria*, mammals *Cervus elaphus*, *Marmota flaviventer*, birds *Cyanistes caeruleus*, *Parus major*, fish *Salmo salar L.*, Table S2). These studies highlight the value of phenotypic characterization, giving crucial insights into both the selection pressures that climate change exerts on populations as well as insights into the factors and constraints that determine the likelihood of adaptation. For example, phenotypic characterization in the winter moth (insect *Operophtera brumata*) revealed that climate change selection occurred through the effect of temperature on the extent of phenological mismatch between the timing of winter moth egg hatching and the timing of its food source, oak budburst (van Asch et al., 2007). These insights could be used to show that the winter moth has been under hard selection: individual fitness consequences of climate change selection also negatively affected winter moth population growth rates despite density-dependent population dynamics, which could have been a driver of rapid adaptation (van Dis et al., 2023). In contrast, in the great tit (bird *Parus major*), fitness consequences of climate change in spring are buffered by population density-dependent survival in winter (Reed et al., 2013), which could mean that the lack of genetic change despite climate change selection [(Gienapp et al., 2006; Ramakers et al., 2019), Table 3)] might be explained by selection not yet being strong enough to overcome buffering mechanisms to induce rapid evolution.

Population-specific responses

Studies that tested but did not find genetic change in wild populations under climate change mostly involved species with longer generation times and traits with a weak genetic basis (i.e. low heritability, Table 3), which could constrain these populations to adapt to climate change by lowering the rate of adaptation (Chevin et al., 2010). Interestingly, some of the species that were not found to have genetically changed under climate change, were found to have genetically changed in other populations for the same studied traits (i.e. plants *Arabidopsis thaliana* and scarlet monkeyflower *Mimulus cardinalis*, Table 2 and 3), while for the other six species only one or two populations have been studied (Table 3). Similarly, studies that investigated replicate populations often found population differences in the magnitude of phenotypic and/or genetic change over time (e.g. fish *Gasterosteus aculeatus*, insect *Wyeomyia smithii*, plants *Clarkia xantiana*, *Cyanus segetum*, reptile *Anolis carolinensis*, Table 2). For example, in plants, several studies found that genetic adaptation in response to drought was less pronounced or absent in populations that historically experienced drier conditions (Franks et al., 2007; Lambrecht et al., 2020; Spurlin & Lambrecht, 2024). While in some cases these contrasting results could be due to methodological caveats (e.g. no refresher generation used for resurrection studies or low-powered statistical tests, see Table S2), these studies strengthen the idea that responses to climate change are population specific. Populations that are not (yet) adapting to climate change might, for example, be constrained by fluctuating selection (Jantzen & Visser, 2023). Fluctuating selection might also hamper the rate of adaptation through adaptation reversal (Hamann et al., 2018) or conversely promote long-term adaptive potential to climatic change by maintaining genetic variation (Johnson et al., 2023). For example, in field mustard (plant *Brassica rapa*), increased temporal replication – from two to four timepoints – allowed for capturing two drought periods, confirming that drought was the selection pressure behind the observed phenotypic change: both post-drought generations flowered earlier. However, intervening wet seasons reversed these adaptations (Hamann et al., 2018). Note that if these populations had only been sampled at two timepoints, with the second timepoint after an intervening wet season, genetic change might have gone undetected for this species. Continued long-term monitoring is needed to determine how this fluctuating selection influences the populations' long-term adaptative potential to climate change.

3.2 Strength of evidence

Slow but accumulating evidence

Compared to the last systematic literature review on natural populations genetically adapting to climate change [(Merilä & Hendry, 2014) and references therein], 29 species were newly identified to have genetically changed in response to climate change in the last decade (Table 2), in addition to five new species tested for genetic change but not found to have changed (Table 3). Especially resurrection experiments are taking off to strongly infer genetic change over time (criterium 1; N=19 new studies of plants, Daphnia species, and a dinoflagellate), followed by molecular genetic approaches (N=7 studies), quantitative genetics using animal models (N=4 studies of mostly longer-lived species), and common garden experiments repeated over time (N=3 of mostly shorter-lived species, Table S2). Nevertheless, relative to the vast number of species and populations subjected to climate change (IPCC, 2022), 49 species for which genetic change has been strongly inferred is still relatively few (but see below for additional species with suggestive evidence). As pointed out by many before [e.g. (Charmantier & Gienapp, 2014; Lovell et al., 2023; Merilä & Hendry, 2014; Urban et al., 2024)], the reason for this scarcity is most likely technical: long-term data are generally rare and difficult to obtain

(Estes et al., 2018; Lindenmayer, 2018; Lovell et al., 2023) and applying strong inference methods such as resurrection experiments, repeated experimentation, and individual tracking needed for applying animal models (i.e. strong methods criterium 1, Table 1) can be impossible or hard to implement for many – especially long-lived – species (Charmantier & Gienapp, 2014; Merilä & Hendry, 2014). Nevertheless, this review shows that our continued effort on this front is slowly accumulating evidence of the importance of genetic adaptation for population responses to climate change, lending extra weight to the recent calls to initiate and maintain long-term monitoring of wild populations that specifically allows for strongly inferring genetic change over time in response to climate change (Cocciardi et al., 2024; Jensen & Leigh, 2022; Urban et al., 2024).

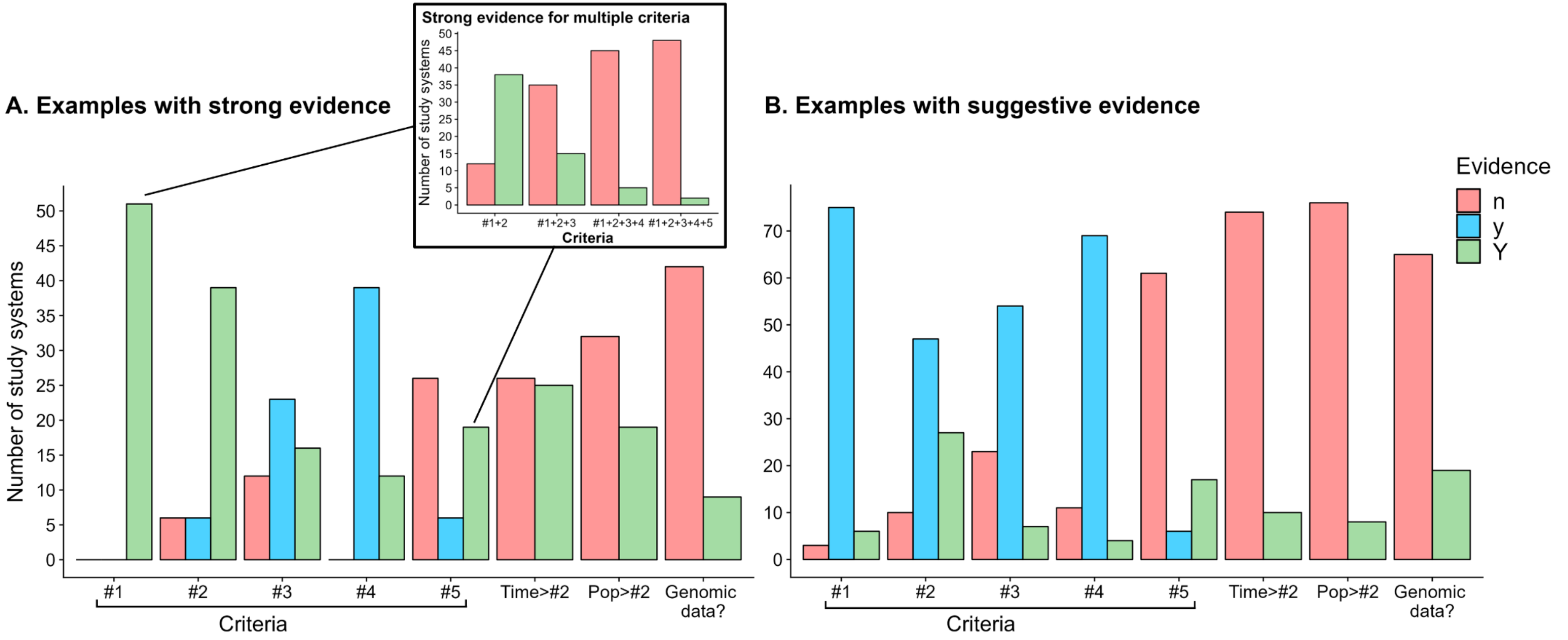


Figure 2. Evidence for genetic adaptation driven by climate change. Shown are the number of study systems that meet the criteria* to demonstrate that a wild population is genetically adapting to climate change. **A)** Examples with strong inference of genetic change over time, with the inset showing the number of studies with strong evidence for multiple criteria (see Table 2 and 3). **B)** Examples with suggestive but not yet strong evidence (see Table S3). Study systems with sufficient temporal and spatial replication (i.e. at least 3 time points and populations sampled) as well as studies with genomic data present important opportunities to strengthen our evidence base of genetic adaptation responses to climate change (see main text). Note the different scales on the y-axes.

**Criteria: (1) population shows genetic change over time, (2) a phenotypic change over time occurred, (3) the fitness of the phenotype depends on a climatic variable, (4) climate change-induced selection occurred across generations, and (5) the relative contribution of adaptive and neutral evolutionary processes has been determined. Evidence: Blue ('y') = yes, Red ('n') = no; Green ('Y') = Yes using strong inference methods (see Table 1 and S2).*

Promise of temporal genomics approaches

The advent of applying genomics approaches to non-model species opens the door to also test for genetic adaptation to climate change in species for which the phenotype under selection is not yet known or for which other strong inference methods are difficult to implement (criterium 1, see above), as well as allowing us to gain important insights into the process and rate of evolution (Clark et al., 2023; Waldvogel et al., 2020). Indeed, in the last decade, studies have started to use temporal genomics to assess genetic adaptation to climate change and investigate which genomic regions and underlying genes are under climate change-induced selection (Fig. 2A; N=9: 3 plants, 1 alga, 1 bird, 1 crustacean, 1 fish, 1 mammal, and 1 reptile). Together, these few genomics studies already cover a diverse range of traits in different species as well as different climate change-induced selection pressures (Table 2 and 3). The observed patterns indicate that climate change adaptation seems to involve multiple targets of selection – and often distinct genetic bases leading to similar phenotypic evolution – with a potential role for local adaptation and admixture as sources of genetic variation [(Campbell-Staton et al., 2017; Frachon et al., 2017; Franks et al., 2016; Hamann et al., 2021; Jump et al., 2006; Turbek et al., 2023), Table S2]. Interestingly, one study also found that especially loci with an intermediate degree of pleiotropy showed the largest temporal differentiation (Frachon et al., 2017), thus indicating that the presence of variation at such loci might be an important factor determining the rate of evolution. However, so far, only one of these nine genomics studies performed variant analysis for more than two time points (i.e. more timepoints than just before and after climate change-selection): for the plant *Fagus sylvatica*, amplified fragment length polymorphism (AFLP) molecular markers (N=254) were analysed for four timepoints, indicating one outlier locus whose allele frequency covaried with temperature. Although the number of markers is low, this study highlights the power of high-resolution temporal genomics: variant analysis for more than two time points allows for studying allele frequency trajectories and empirically testing underlying drivers (Barghi et al., 2020; Clark et al., 2023).

One particularly important aspect that genomics approaches can help with is assessing the relative contribution of different evolutionary processes underlying the observed genetic change (criterium 5). Interestingly, a recent poll among researchers in the field of climate change adaptation indicated that gene flow is considered as the most important mechanism facilitating adaptive responses to climate change (Urban et al., 2024). However, to date, less than half of the studies have strongly inferred the relative contribution of response to selection, gene flow and drift to genetic adaptation to climate change (N=19, Fig. 2A and Table 2 and 3). Studies that have used strong inference to assess this relative contribution most often used genomics approaches (N=14), followed by absolute population tracking (N=3), and animal models (N=2), with so far only two studies finding evidence for gene flow to be an important mechanism (Turbek et al., 2023; Valencia-Montoya et al., 2021), while the other studies indicate that selection on standing genetic variation underlies the observed genetic changes (Bonnet et al., 2019; Campbell-Staton et al., 2021; Frachon et al., 2017; Henning-Lucass et al., 2016; Karell et al., 2011; Reynes et al., 2024; Welt et al., 2015). Naturally, more studies assessing criterium 5 (Table 1) are needed to confirm whether this is indeed a general pattern.

Importance of combining field observations with experimentation

While increased long-term monitoring and the application of temporal genomics approaches would allow for extending tests of genetic change over time to many more species and ecosystems (see above), it is important that such efforts are followed up by phenotypic characterizations and experimentation (criteria 2 and 3). Indeed, the few studies with strong evidence for climate change being the causal driver (criterium 4, N=12; Fig. 2A), used information about the phenotype under selection to explicitly test how selection estimates changed in the field (e.g. bird *Strix aluco*, insect *Operophtera brumata*, mammal *Cervus* *elaphus* and plant *Clarkia xantiana*) or by replicating the observed response with experimental evolution (crustacean *Daphnia magna*, Table 2 and 3). The need for experimentation is further exemplified by the case studies with the strongest evidence for genetic adaptation to climate change, having used strong inference methods for criteria 1-4 (insect *Operophtera brumata* and plants *Clarkia xantiana* and *Thymus vulgaris*) or all 5 criteria (crustacean *Daphnia magna* and plant *Brassica rapa*, Table 2): all include evidence obtained via experimentation to establish that climate variables induce fitness consequences, allowing for strong inference that the observed phenotypic changes are adaptive and in response to climate change selection. With only five examples that robustly tested for genetic adaptation to climate change, there are ample opportunities available for the other 44 species with strong evidence for criterium 1, but not yet for criteria 2-5 (Table 2 and 3), to further supplement their evidence base to corroborate that the observed genetic changes are indeed adaptive under climate change. While not possible for all species, strengthening these existing examples of genetic adaptation is needed to inform the prediction of population responses to climate change, as an intimate understanding of which phenotypes are under selection, the fitness consequences of that selection, and how phenotypes map to genotypes is considered essential for improving such predictions (Garcia-Costoya et al., 2023; Urban et al., 2024). For example, take the cline shifts in polymorphism molecular markers that were found for three different *Drosophila* species (Table 2): repeated sampling across both time and space, combined with the fact that these polymorphisms correlate with latitude and temperature across space, makes it highly likely that the observed genetic changes are in response to climate change – highlighting that genomics approaches with good spatial and/or temporal replication are a promising approach to assess genetic responses to climate change in many more species and ecosystems (see discussion above and below). However, while it is clear from these examples that *Drosophila* populations are genetically responding, relying on correlative patterns in molecular genetic data alone can lead to spurious inferences [e.g. (Berg et al., 2019; Fitzpatrick et al., 2018)], and without follow-up phenotypic characterization, it is hard to say what is happening. What aspect of climate change is driving the observed changes? Is it direct or indirect selection? Are the observed changes adaptive and mainly driven by changes in standing variation in response to selection or are we observing repeated range shifting? Answers to these questions are needed to be able to use these examples for predicting population responses.

Improving spatial and temporal replication

As outlined and exemplified in this review, sufficient temporal and spatial replication is needed to (1) establish that populations are indeed adapting to climate change rather than to individual climate fluctuations or other environmental drivers, (2) to distinguish between response to selection and genetic drift, and (3) to gain insights into what determines a population's adaptive potential. While temporal and spatial replication is generally still low – currently half of the 51 included studies sampled more than two timepoints (N=25) and less than half of the studies assessed genetic adaptation to climate change in at least three populations (N=19), with very few species having both spatial and temporal replication (N=7 with >2 timepoints and >2 populations, Fig. 2A, Table 2 and 3) – with sufficient temporal and spatial replication, the identified examples present exciting opportunities to further elucidate the drivers and constraints that determine the likelihood and rate of adaptation to climate change in wild populations. For example, comparing replicate populations on aspects such as selection strength, the level of standing genetic variation, and/or population dynamics to empirically test how these factors influence the likelihood of evolutionary rescue. Moreover, increased temporal replication would provide important information about the process and rate of evolution that studies with only two timepoints are missing (Barghi et al., 2020), allowing us to empirically test which factors drive the rate of adaptation in wild populations. For example, how do gene flow, opposing selection pressures, and the genetic architecture of the trait under selection facilitate or hamper the rate of adaption? Finally, increased replication would allow for testing the assumption that local adaptation patterns (i.e. the spatial relationships observed between climate and biotic responses across a species range) are a good predictor of adaptive capacity. Due to the lack of long-term temporal data, such space-for-time substitutions are frequently used to make predictions about population responses to future climate change [Tables S1; (Lovell et al., 2023)]. For example, spatial patterns observed in key traits or genomic variation that correlate with temperature or precipitation are used to predict population responses to climate change [e.g. (Bay et al., 2018; Miller et al., 2020)], assuming that the observed phenotypic and/or genetic variation underlying these spatial patterns are predictive of changes that will happen in response to climate change over time. However, this assumption of space-time equivalence has rarely been tested (Lovell et al., 2023). I urge the field to capitalize on and strengthen the existing examples of genetic adaptation to climate change identified here (Table 2 and 3), allowing us to start testing these pressing questions by assessing and comparing spatial and temporal signatures of climate selection.

Low-hanging fruit to extend ecological and taxonomic representation

Like the previous review, this review has focused on studies that used strong inference methods to infer genetic change over time (criterium 1, Table 1), as only these methods provide conclusive evidence for evolutionary responses (Hansen et al., 2012; Merilä & Hendry, 2014). However, many more studies were identified that attempted to assess genetic adaptation to climate change in wild populations over time (Table S2). These studies provide additional suggestive evidence that genetic adaptation plays an important role in population responses to climate change (Figure 2B, N=42 papers), encompassing 84 additional species (Table S3, genetic change: 53 plants, 9 insects, 3 birds, 1 mammal, 1 arachnid, 1 fish, 1 phytoplankton; no genetic change: 12 plants, 3 birds). With targeted follow-up studies to supplement their evidence base, these suggestive studies could similarly provide important opportunities to determine the drivers and constraints that underly adaptive potential under climate change. The lowest-hanging fruit are studies that used a repeated common-garden experiment over time but that did not yet account for maternal (and storage) effects [N=14 papers for 70 additional species, e.g. (Helm et al., 2019; Higgins et al., 2014; Nielsen et al., 2023); and plant resurrection experiments without a refresher generation e.g. (Everingham et al., 2021; Gómez et al., 2018; Nevo et al., 2012); Table S2]. I recommend supplementing these studies with additional evidence for the genetic basis of the trait, such as obtaining heritability estimates via breeding experiments or by utilizing genomic data (Table 1), to similarly strongly infer genetic adaptation to climate change. For plants, ecological and taxonomic representation can furthermore be easily extended through Project Baseline: a USA seed bank collected in 2015 with good spatial replication (i.e. 10-20 populations sampled per species), specifically designed for resurrection experiments to assess genetic adaptation over time [(Etterson et al., 2016), currently at 65 species, (http://www.baselineseedbank.org/, accessed 2024-11-06)]. Similarly, species with populations for which phenotypic and/or genotypic characterizations have already been performed at one time point, such as space-for-time substitutions studies (Lovell et al., 2023), represent important opportunities for resampling and testing for genetic change over time.

Significant opportunities exist for range shifting populations. While I assessed several papers on genetic adaption in range shifting populations (N=10 papers for 7 species: 4 insects, 1 mammal, 1 arachnid, 1 plant; Table S2 and S3), only one study sampled populations at more than one timepoint (Bi et al., 2019). However, the temporal comparison in this study was between different parts of the species’ range: the modern sample consisted of a different part of the range than the historic sample. Because such a comparison cannot distinguish genetic adaptation from other processes such as nonrandom dispersal and founder effects, this study does not yet meet the criteria for showing genetic adaptation to climate change over time. As range shifting is being observed for many species (Lenoir & Svenning, 2015; Parmesan & Yohe, 2003), I recommend resampling range-shifting populations in the future to investigate genetic adaptation to climate change in these wild populations. Such studies should pay particular attention to sampling design to ensure temporal comparisons that can distinguish spatial sorting and founder effects from genetic adaptation (i.e. comparing the same location and the same part of the range).

4. Conclusions and future directions

To avoid population extinction, organisms need to be able to genetically adapt at a rate that allows them to keep up with the rate of climate change (Gonzalez et al., 2013; Visser, 2008). To improve our ability to predict such evolutionary rescue, we need to (1) assess genetic adaptation to climate change in a wider variety of species and ecosystems (Urban et al., 2024) and (2) capitalize on existing examples of genetic adaptation to advance our knowledge on the drivers and constraints underlying climate change adaptation (this review). To guide these efforts, this review gathered examples of wild populations for which genetic adaptation to climate change has so far been strongly inferred, identifying 51 case studies of 49 species (Table 2 and 3). While taxonomic and ecosystem diversification is clearly needed for the future (Fig.1), this comprehensive overview shows that the field's continued effort is slowly accumulating evidence of the importance of genetic adaptation for population responses to climate change. Emerging patterns indicate that these genetic responses are often population specific and related to shifts in temperature and precipitation regimes, both through direct effects on survival and reproduction and indirect effects through changing species interactions. These studies furthermore suggest that fluctuating selection, population buffering (e.g. density-dependent population dynamics), the strength of selection, generation time, preadaptation, and standing genetic variation are important factors influencing the likelihood and rate of adaptation.

By also assessing the strength of evidence for genetic adaptation to climate change in the 51 existing case studies (Fig.2), I identified several key opportunities for the field to supplement and strengthen our evidence base. An easy place to start extending ecological and taxonomic representation and to further validate the frequency of genetic adaptation under climate change, are the identified studies of an additional 84 species that used suggestive but not yet strong methods for inferring genetic adaptation to climate change (Table S3, Fig.2B). Moreover, few studies have so far used temporal genomics approaches (Fig.2), while these approaches would allow for assessing genetic adaptation to climate change in many more species, as well as studying allele frequency trajectories to gain insights into the process and rate of evolution (Barghi et al., 2020). It is important that such efforts are followed up by phenotypic characterizations and experimentation, as so far, only five of the 51 identified case studies robustly demonstrated genetic adaptation driven by climate change (Table 2 and Fig.2A). These examples show that using strong inference – to demonstrate that the observed genetic changes are indeed adaptive and in response to climate change (Table 1) – provides crucial insights into the selection pressures and fitness consequences that climate change exerts; information that is highly needed to accurately predict population responses (Garcia-Costoya et al., 2023; Urban et al., 2024). To allow for synthesis and meta-analysis, it is also important that raw data are made openly available, which many studies have not yet done (N=22 studies without raw data, Table 2 and 3). Finally, increased spatial and temporal replication are needed, not only to prevent erroneous conclusions about the environmental drivers and evolutionary processes underlying the observed genetic changes, but also to allow for the exciting opportunity to start empirically testing and validating drivers and constraints underlying the likelihood and rate of genetic adaptation to climate change.

Acknowledgements

I would like to thank my advisors Marcel E. Visser and Bregje Wertheim for their constructive criticism and valuable advice on this manuscript. I would also like to thank Marjo Saastamoinen for helpful discussion, and Evolution editors Ophelie Ronce, Ruth Shaw, and XX anonymous reviewers for their constructive comments to improve the manuscript. This research was supported by an Adaptive Life Program grant (IVA AL 3.2C DIS) made possible by the Board of the University of Groningen, the Faculty of Science and Engineering, and the Groningen Institute for Evolutionary Life Science (GELIFES). I was furthermore supported during the preparation of this manuscript by the Novo Nordisk Challenge Programme grant number NNF20OC0060118.

Conflict of interest

The author has no conflict of interest to declare.

Data availability statement

All Web of Science (WoS) records assessed, including descriptions and summaries for selection and inclusion, can be found in the supplementary material (Tables S1a, S1b and S2). The WoS search expressions used to perform the systematic literature review, the raw WoS output, and the scripts used for data wrangling and producing tables and figures are available in the Dryad digital repository (van Dis, 2025). link for reviewer access: https://datadryad.org/stash/share/TgwQjK3o_47GnWjLcwaDn-YgtzCe8kCMwGJ7HQL4Hqc

References

Anstett, D. N., Branch, H. A., & Angert, A. L. (2021). Regional differences in rapid evolution during severe drought. *Evolution Letters*, *5*(2), 130–142. https://doi.org/10.1002/evl3.218

Bailey, L. D., van de Pol, M., Adriaensen, F., Arct, A., Barba, E., Bellamy, P. E., Bonamour, S., Bouvier, J. C., Burgess, M. D., Charmantier, A., Cusimano, C., Doligez, B., Drobniak, S. M., Dubiec, A., Eens, M., Eeva, T., Ferns, P. N., Goodenough, A. E., Hartley, I. R., … Visser, M. E. (2022). Bird populations most exposed to climate change are less sensitive to climatic variation. *Nature Communications*, *13*(1), 1–10. https://doi.org/10.1038/s41467-022-29635-4

Balanya, J., Oller, J. M., Huey, R. B., Gilchrist, G. W., & Serra, L. (2006). Global Genetic Change Tracks Global Climate Warming in Drosophila subobscura. *Science*, *313*, 1773–1775. https://doi.org/10.1126/science.1131002

Barghi, N., Hermisson, J., & Schlötterer, C. (2020). Polygenic adaptation: a unifying framework to understand positive selection. *Nature Reviews Genetics*, *21*(12), 769–781. https://doi.org/10.1038/s41576-020-0250-z

Bay, R. A., Harrigan, R. J., Underwood, V. Le, Gibbs, H. L., Smith, T. B., & Ruegg, K. (2018). Genomic signals of selection predict climate-driven population declines in a migratory bird. *Science*, *359*(6371), 83–86. https://doi.org/10.1126/science.aan4380

Benning, J. W., Faulkner, A., & Moeller, D. A. (2023). Rapid evolution during climate change: demographic and genetic constraints on adaptation to severe drought. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1998). https://doi.org/10.1098/rspb.2023.0336

Berg, J. J., Harpak, A., Sinnott-Armstrong, N., Joergensen, A. M., Mostafavi, H., Field, Y., Boyle, E. A., Zhang, X., Racimo, F., Pritchard, J. K., & Coop, G. (2019). Reduced signal for polygenic adaptation of height in UK biobank. *ELife*, *8*, 1–47. https://doi.org/10.7554/eLife.39725

Besnier, F., Skaala, Ø., Wennevik, V., Ayllon, F., Utne, K. R., Fjeldheim, P. T., Andersen-Fjeldheim, K., Knutar, S., & Glover, K. A. (2024). Overruled by nature: A plastic response to environmental change disconnects a gene and its trait. *Molecular Ecology*, *33*(2), 1–12. https://doi.org/10.1111/mec.16933

Bi, K., Linderoth, T., Singhal, S., Vanderpool, D., Patton, J. L., Nielsen, R., Moritz, C., & Good, J. M. (2019). Temporal genomic contrasts reveal rapid evolutionary responses in an alpine mammal during recent climate change. *PLOS Genetics*, *15*(5), e1008119. https://doi.org/10.1371/journal.pgen.1008119

Biquet, J., Bonamour, S., de Villemereuil, P., de Franceschi, C., & Teplitsky, C. (2022). Phenotypic plasticity drives phenological changes in a Mediterranean blue tit population. *Journal of Evolutionary Biology*, *35*(2), 347–359. https://doi.org/10.1111/jeb.13950

Blanckenhorn, W. U. (2015). Investigating yellow dung fly body size evolution in the field: Response to climate change? *Evolution*, *69*(8), 2227–2234. https://doi.org/10.1111/evo.12726

Bonamour, S., Chevin, L. M., Charmantier, A., & Teplitsky, C. (2019). Phenotypic plasticity in response to climate change: The importance of cue variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1768). https://doi.org/10.1098/rstb.2018.0178

Bonnet, T., Morrissey, M. B., Morris, A., Morris, S., Clutton-Brock, T. H., Pemberton, J. M., & Kruuk, L. E. B. (2019). The role of selection and evolution in changing parturition date in a red deer population. *PLoS Biology*, *17*(11), 1–23. https://doi.org/10.1371/journal.pbio.3000493

Bonnet, T., Wandeler, P., Camenisch, G., & Postma, E. (2017). Bigger Is Fitter? Quantitative Genetic Decomposition of Selection Reveals an Adaptive Evolutionary Decline of Body Mass in a Wild Rodent Population. *PLoS Biology*, *15*(1), 1–21. https://doi.org/10.1371/journal.pbio.1002592

Bradshaw, W. E., & Holzapfel, C. M. (2001). Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences*, *98*(25), 14509–14511. https://doi.org/10.1073/pnas.241391498

Brakefield, P. M., & De Jong, P. W. (2011). A steep cline in ladybird melanism has decayed over 25 years: A genetic response to climate change. *Heredity*, *107*(6), 574–578. https://doi.org/10.1038/hdy.2011.49

Branch, H. A., Anstett, D. N., & Angert, A. L. (2024). Phenotypic lags influence rapid evolution throughout a drought cycle. *Evolution*, *78*(6), 1067–1077. https://doi.org/10.1093/evolut/qpae037

Cameron, R. A. D., & Cook, L. M. (2013). Temporal morph frequency changes in sand-dune populations of Cepaea nemoralis (L.). *Biological Journal of the Linnean Society*, *108*(2), 315–322. https://doi.org/10.1111/j.1095-8312.2012.02008.x

Cameron, R. A. D., & Pokryszko, B. M. (2008). Variation in Cepaea populations over 42 years: Climate fluctuations destroy a topographical relationship of morph-frequencies. *Biological Journal of the Linnean Society*, *95*(1), 53–61. https://doi.org/10.1111/j.1095-8312.2008.01042.x

Campbell-Staton, S. C., Cheviron, Z. A., Rochette, N., Catchen, J., Losos, J. B., & Edwards, S. V. (2017). Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. *Science*, *357*(6350), 495–498. https://doi.org/10.1126/science.aam5512

Campbell-Staton, S. C., Velotta, J. P., & Winchell, K. M. (2021). Selection on adaptive and maladaptive gene expression plasticity during thermal adaptation to urban heat islands. *Nature Communications*, *12*(1), 1–14. https://doi.org/10.1038/s41467-021-26334-4

Carroll, S. P., Hendry, A. P., Reznick, D. N., & Fox, C. W. (2007). Evolution on ecological time-scales. *Functional Ecology*, *21*(3), 387–393. https://doi.org/10.1111/j.1365-2435.2007.01289.x

Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evolutionary Applications*, *7*, 15–28. https://doi.org/10.1111/eva.12126

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*(5877), 800–803. https://doi.org/10.1126/science.1157174

Cheptou, P. O., Imbert, E., & Thomann, M. (2022). Rapid evolution of selfing syndrome traits in Viola arvensis revealed by resurrection ecology. *American Journal of Botany*, *109*(11), 1838–1846. https://doi.org/10.1002/ajb2.16028

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. *PLoS Biology*, *8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Clark, R. D., Catalano, K. A., Fitz, K. S., Garcia, E., Jaynes, K. E., Reid, B. N., Sawkins, A., Snead, A. A., Whalen, J. C., & Pinsky, M. L. (2023). The practice and promise of temporal genomics for measuring evolutionary responses to global change. *Molecular Ecology Resources*, *March*, 1–17. https://doi.org/10.1111/1755-0998.13789

Cocciardi, J. M., Hoffman, A. M., Alvarado-Serrano, D. F., Anderson, J., Blumstein, M., Boehm, E. L., Bolin, L. G., Borokini, I. T., Bradburd, G. S., Branch, H. A., Brudvig, L. A., Chen, Y., Collins, S. L., Des Marais, D. L., Gamba, D., Hanan, N. P., Howard, M. M., Jaros, J., Juenger, T. E., … Avolio, M. L. (2024). The value of long-term ecological research for evolutionary insights. *Nature Ecology and Evolution*, *8*(9), 1584–1592. https://doi.org/10.1038/s41559-024-02464-y

Compagnoni, A., Evers, S., & Knight, T. (2024). Spatial replication can best advance our understanding of population responses to climate. *Ecography*, *2024*(1), 1–8. https://doi.org/10.1111/ecog.06833

Cook, L. M., & Saccheri, I. J. (2013). The peppered moth and industrial melanism: evolution of a natural selection case study. *Heredity*, *110*(3), 207–212. https://doi.org/10.1038/hdy.2012.92

Cowie, R. H., & Jones, J. S. (1998). Gene frequency changes in Cepaea snails on the Marlborough Downs over 25 years. *Biological Journal of the Linnean Society*, *65*(3), 233–255. https://doi.org/10.1006/bijl.1998.0250

Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., & Primmer, C. R. (2022). Rapid evolution in salmon life history induced by direct and indirect effects of fishing. *Science*, *376*(6591), 420–423. https://doi.org/10.1126/science.abg5980

Des Roches, S., Bell, M. A., & Palkovacs, E. P. (2020). Climate-driven habitat change causes evolution in Threespine Stickleback. *Global Change Biology*, *26*(2), 597–606. https://doi.org/10.1111/gcb.14892

Dickman, E. E., Pennington, L. K., Franks, S. J., & Sexton, J. P. (2019). Evidence for adaptive responses to historic drought across a native plant species range. *Evolutionary Applications*, *12*(8), 1569–1582. https://doi.org/10.1111/eva.12803

Dunn, P. O., Ahmed, I., Armstrong, E., Barlow, N., Barnard, M. A., Bélisle, M., Benson, T. J., Berzins, L. L., Boynton, C. K., Brown, T. A., Cady, M., Cameron, K., Chen, X., Clark, R. G., Clotfelter, E. D., Cromwell, K., Dawson, R. D., Denton, E., Forbes, A., … Whittingham, L. A. (2023). Extensive regional variation in the phenology of insects and their response to temperature across North America. *Ecology*, *104*(5), 1–17. https://doi.org/10.1002/ecy.4036

Eizaguirre, C., & Baltazar-Soares, M. (2014). Evolutionary conservation-evaluating the adaptive potential of species. *Evolutionary Applications*, *7*(9), 963–967. https://doi.org/10.1111/eva.12227

Endler, J. A. (1986). *Natural Selection in the Wild. (MPB-21), Volume 21*. Princeton University Press. https://doi.org/10.12987/9780691209517

Estes, L., Elsen, P. R., Treuer, T., Ahmed, L., Caylor, K., Chang, J., Choi, J. J., & Ellis, E. C. (2018). The spatial and temporal domains of modern ecology. *Nature Ecology and Evolution*, *2*(5), 819–826. https://doi.org/10.1038/s41559-018-0524-4

Etges, W. J., & Levitan, M. (2008). Variable evolutionary response to regional climate change in a polymorphic species. *Biological Journal of the Linnean Society*, *95*(4), 702–718. https://doi.org/10.1111/j.1095-8312.2008.01092.x

Etterson, J. R., Franks, S. J., Mazer, S. J., Shaw, R. G., Gorden, N. L. S., Schneider, H. E., Weber, J. J., Winkler, K. J., & Weis, A. E. (2016). Project Baseline: An unprecedented resource to study plant evolution across space and time. *American Journal of Botany*, *103*(1), 164–173. https://doi.org/10.3732/ajb.1500313

Evans, S. R., & Gustafsson, L. (2017). Climate change upends selection on ornamentation in a wild bird. *Nature Ecology & Evolution*, *1*(2), 0039. https://doi.org/10.1038/s41559-016-0039

Everingham, S. E., Offord, C. A., Sabot, M. E. B., & Moles, A. T. (2021). Time-traveling seeds reveal that plant regeneration and growth traits are responding to climate change. *Ecology*, *102*(3), 1–15. https://doi.org/10.1002/ecy.3272

Fitzpatrick, M. C., Keller, S. R., & Lotterhos, K. E. (2018). Comment on “Genomic signals of selection predict climate-driven population declines in a migratory bird”. *Science*, *361*(6401), 2–3. https://doi.org/10.1126/science.aat7279

Frachon, L., Libourel, C., Villoutreix, R., Carrère, S., Glorieux, C., Huard-Chauveau, C., Navascués, M., Gay, L., Vitalis, R., Baron, E., Amsellem, L., Bouchez, O., Vidal, M., Le Corre, V., Roby, D., Bergelson, J., & Roux, F. (2017). Intermediate degrees of synergistic pleiotropy drive adaptive evolution in ecological time. *Nature Ecology & Evolution*, *1*(10), 1551–1561. https://doi.org/10.1038/s41559-017-0297-1

Franks, S. J. (2011). Plasticity and evolution in drought avoidance and escape in the annual plant Brassica rapa. *New Phytologist*, *190*(1), 249–257. https://doi.org/10.1111/j.1469-8137.2010.03603.x

Franks, S. J., & Hoffmann, A. A. (2012). Genetics of Climate Change Adaptation. *Annual Review of Genetics*, *46*(1), 185–208. https://doi.org/10.1146/annurev-genet-110711-155511

Franks, S. J., Kane, N. C., O’Hara, N. B., Tittes, S., & Rest, J. S. (2016). Rapid genome-wide evolution in Brassica rapa populations following drought revealed by sequencing of ancestral and descendant gene pools. *Molecular Ecology*, *25*(15), 3622–3631. https://doi.org/10.1111/mec.13615

Franks, S. J., Sim, S., & Weis, A. E. (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences*, *104*(4), 1278–1282. https://doi.org/10.1073/pnas.0608379104

Franks, S. J., & Weis, A. E. (2008). A change in climate causes rapid evolution of multiple life-history traits and their interactions in an annual plant. *Journal of Evolutionary Biology*, *21*(5), 1321–1334. https://doi.org/10.1111/j.1420-9101.2008.01566.x

Garcia-Costoya, G., Williams, C. E., Faske, T. M., Moorman, J. D., & Logan, M. L. (2023). Evolutionary constraints mediate extinction risk under climate change. *Ecology Letters*, *26*(4), 529–539. https://doi.org/10.1111/ele.14173

Geerts, A. N., Vanoverbeke, J., Vanschoenwinkel, B., Van Doorslaer, W., Feuchtmayr, H., Atkinson, D., Moss, B., Davidson, T. A., Sayer, C. D., & De Meester, L. (2015). Rapid evolution of thermal tolerance in the water flea Daphnia. *Nature Climate Change*, *5*(7), 665–668. https://doi.org/10.1038/nclimate2628

Gienapp, P., Postma, E., & Visser, M. E. (2006). Why breeding time has not responded to selection for earlier breeding in a songbird population. *Evolution*, *60*(11), 2381. https://doi.org/10.1554/06-235.1

Gómez, R., Méndez-Vigo, B., Marcer, A., Alonso-Blanco, C., & Picó, F. X. (2018). Quantifying temporal change in plant population attributes: Insights from a resurrection approach. *AoB PLANTS*, *10*(5), 1–17. https://doi.org/10.1093/aobpla/ply063

Gonzalez, A., Ronce, O., Ferriere, R., & Hochberg, M. E. (2013). Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1610), 20120404. https://doi.org/10.1098/rstb.2012.0404

Grant, B. R., & Grant, P. R. (2003). What Darwin's Finches Can Teach Us about the Evolutionary Origin and Regulation of Biodiversity. *BioScience*, *53*(10), 965–975.

Hamann, E., Pauli, C. S., Joly-Lopez, Z., Groen, S. C., Rest, J. S., Kane, N. C., Purugganan, M. D., & Franks, S. J. (2021). Rapid evolutionary changes in gene expression in response to climate fluctuations. *Molecular Ecology*, *30*(1), 193–206. https://doi.org/10.1111/mec.15583

Hamann, E., Weis, A. E., & Franks, S. J. (2018). Two decades of evolutionary changes in brassica rapa in response to fluctuations in precipitation and severe drought. *Evolution*, *72*(12), 2682–2696. https://doi.org/10.1111/evo.13631

Hansen, M. M., Olivieri, I., Waller, D. M., & Nielsen, E. E. (2012). Monitoring adaptive genetic responses to environmental change. *Molecular Ecology*, *21*(6), 1311–1329. https://doi.org/10.1111/j.1365-294X.2011.05463.x

Harvey, A., Skaala, Ø., Borgstrøm, R., Fjeldheim, P. T., Christine Andersen, K., Rong Utne, K., Askeland Johnsen, I., Fiske, P., Winterthun, S., Knutar, S., Sægrov, H., Urdal, K., & Alan Glover, K. (2022). Time series covering up to four decades reveals major changes and drivers of marine growth and proportion of repeat spawners in an Atlantic salmon population. *Ecology and Evolution*, *12*(4), 1–13. https://doi.org/10.1002/ece3.8780

Helm, B., Van Doren, B. M., Hoffmann, D., & Hoffmann, U. (2019). Evolutionary Response to Climate Change in Migratory Pied Flycatchers. *Current Biology*, *29*(21), 3714-3719.e4. https://doi.org/10.1016/j.cub.2019.08.072

Henning-Lucass, N., Cordellier, M., Streit, B., & Schwenk, K. (2016). Phenotypic plasticity in life-history traits of Daphnia galeata in response to temperature - a comparison across clonal lineages separated in time. *Ecology and Evolution*, *6*(4), 881–891. https://doi.org/10.1002/ece3.1924

Higgins, J. K., MacLean, H. J., Buckley, L. B., & Kingsolver, J. G. (2014). Geographic differences and microevolutionary changes in thermal sensitivity of butterfly larvae in response to climate. *Functional Ecology*, *28*(4), 982–989. https://doi.org/10.1111/1365-2435.12218

Hinners, J., Kremp, A., & Hense, I. (2017). Evolution in temperature-dependent phytoplankton traits revealed from a sediment archive: Do reaction norms tell the whole story? *Proceedings of the Royal Society B: Biological Sciences*, *284*(1864). https://doi.org/10.1098/rspb.2017.1888

Inouye, D. W., Barr, B., Armitage, K. B., & Inouye, B. D. (2000). Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(4), 1630–1633. https://doi.org/10.1073/pnas.97.4.1630

IPCC. (2022). *Climate Change 2022: Impacts, Adaptation and Vulnerability; Summary for policymakers*. https://doi.org/10.4324/9781315071961-11

Jansen, M., Geerts, A. N., Rago, A., Spanier, K. I., Denis, C., De Meester, L., & Orsini, L. (2017). Thermal tolerance in the keystone species Daphnia magna—a candidate gene and an outlier analysis approach. *Molecular Ecology*, *26*(8), 2291–2305. https://doi.org/10.1111/mec.14040

Jantzen, C. C., & Visser, M. E. (2023). Climate change does not equally affect temporal patterns of natural selection on reproductive timing across populations in two songbird species. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2009). https://doi.org/10.1098/rspb.2023.1474

Jennions, M. D., & Møller, A. P. (2002). Publication bias in ecology and evolution: an empirical assessment using the ‘trim and fill’ method. *Biological Reviews*, *77*(2), 211–222. https://doi.org/10.1017/S1464793101005875

Jensen, E. L., & Leigh, D. M. (2022). Using temporal genomics to understand contemporary climate change responses in wildlife. *Ecology and Evolution*, *12*(9), 1–8. https://doi.org/10.1002/ece3.9340

Johnson, O. L., Tobler, R., Schmidt, J. M., & Huber, C. D. (2023). Fluctuating selection and the determinants of genetic variation. *Trends in Genetics*, *39*(6), 491–504. https://doi.org/10.1016/j.tig.2023.02.004

Jump, A. S., Hunt, J. M., Martínez-Izquierdo, J. A., & Peñuelas, J. (2006). Natural selection and climate change: Temperature-linked spatial and temporal trends in gene frequency in Fagus sylvatica. *Molecular Ecology*, *15*(11), 3469–3480. https://doi.org/10.1111/j.1365-294X.2006.03027.x

Karell, P., Ahola, K., Karstinen, T., Valkama, J., & Brommer, J. E. (2011). Climate change drives microevolution in a wild bird. *Nature Communications*, *2*(1), 207–208. https://doi.org/10.1038/ncomms1213

Karitter, P., March-Salas, M., Ensslin, A., Rauschkolb, R., Godefroid, S., & Scheepens, J. F. (2024). Combining the resurrection approach with transplant experiments to investigate adaptation of plant populations to environmental change. *Perspectives in Plant Ecology, Evolution and Systematics*, *62*(September 2023), 125773. https://doi.org/10.1016/j.ppees.2023.125773

Kołodziejczyk, J., Fijarczyk, A., Porth, I., Robakowski, P., Vella, N., Vella, A., Kloch, A., & Biedrzycka, A. (2025). Genomic investigations of successful invasions: the picture emerging from recent studies. *Biological Reviews*, *100*(3), 1396–1418. https://doi.org/10.1111/brv.70005

Kovach, R. P., Gharrett, A. J., & Tallmon, D. A. (2012). Genetic change for earlier migration timing in a pink salmon population. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1743), 3870–3878. https://doi.org/10.1098/rspb.2012.1158

Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the ‘animal model’. *Phil. Trans. R. Soc. Lond. B*, *359*, 873–890. https://doi.org/10.1098/rstb.2003.1437

Lambrecht, S. C., Gujral, A. K., Renshaw, L. J., & Rosengreen, L. T. (2020). Evolutionary and plastic changes in a native annual plant after a historic drought. *Ecology and Evolution*, *10*(11), 4570–4582. https://doi.org/10.1002/ece3.6156

Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. https://doi.org/10.1111/ecog.00967

Lindenmayer, D. (2018). Why is long-term ecological research and monitoring so hard to do? (And what can be done about it). *Australian Zoologist*, *39*(4), 576–580. https://doi.org/10.7882/AZ.2017.018

Lovell, R. S. L., Collins, S., Martin, S. H., Pigot, A. L., & Phillimore, A. B. (2023). Space-for-time substitutions in climate change ecology and evolution. *Biological Reviews*, *98*(6), 2243–2270. https://doi.org/10.1111/brv.13004

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications*, *7*(1), 1–14. https://doi.org/10.1111/eva.12137

Miller, A. D., Coleman, M. A., Clark, J., Cook, R., Naga, Z., Doblin, M. A., Hoffmann, A. A., Sherman, C. D. H., & Bellgrove, A. (2020). Local thermal adaptation and limited gene flow constrain future climate responses of a marine ecosystem engineer. *Evolutionary Applications*, *13*(5), 918–934. https://doi.org/10.1111/eva.12909

Moyes, K., Nussey, D. H., Clements, M. N., Guinness, F. E., Morris, A., MORRIS, S., Pemberton, J. M., Kruuk, L. E. B., & Clutton-Brock, T. H. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology*, *17*(7), 2455–2469. https://doi.org/10.1111/j.1365-2486.2010.02382.x

Nevo, E., Fu, Y. B., Pavlicek, T., Khalifa, S., Tavasi, M., & Beiles, A. (2012). Evolution of wild cereals during 28 years of global warming in Israel. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(9), 3412–3415. https://doi.org/10.1073/pnas.1121411109

Nielsen, M. E., Nylin, S., Wiklund, C., & Gotthard, K. (2023). Evolution of butterfly seasonal plasticity driven by climate change varies across life stages. *Ecology Letters*, *26*(9), 1548–1558. https://doi.org/10.1111/ele.14280

Norris, L. C., Main, B. J., Lee, Y., Collier, T. C., Fofana, A., Cornel, A. J., & Lanzaro, G. C. (2015). Adaptive introgression in an African malaria mosquito coincident with the increased usage of insecticide-treated bed nets. *Proceedings of the National Academy of Sciences*, *112*(3), 815–820. https://doi.org/10.1073/pnas.1418892112

Ożgo, M., & Schilthuizen, M. (2012). Evolutionary change in Cepaea nemoralis shell colour over 43 years. *Global Change Biology*, *18*(1), 74–81. https://doi.org/10.1111/j.1365-2486.2011.02514.x

Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., & Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, *466*(7305), 482–485. https://doi.org/10.1038/nature09210

Ozgul, A., Tuljapurkar, S., Benton, T. G., Pemberton, J. M., Clutton-Brock, T. H., & Coulson, T. (2009). The Dynamics of Phenotypic Change and the Shrinking Sheep of St. Kilda. *Science*, *325*(5939), 464–467. https://doi.org/10.1126/science.1173668

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change. *Nature*, *421*, 37–42.

Pulido, F., & Berthold, P. (2010). Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(16), 7341–7346. https://doi.org/10.1073/pnas.0910361107

Ramakers, J. J. C., Gienapp, P., & Visser, M. E. (2019). Phenological mismatch drives selection on elevation, but not on slope, of breeding time plasticity in a wild songbird. *Evolution*, *73*(2), 175–187. https://doi.org/10.1111/evo.13660

Rauschkolb, R., Li, Z., Godefroid, S., Dixon, L., Durka, W., Májeková, M., Bossdorf, O., Ensslin, A., & Scheepens, J. F. (2022). Evolution of plant drought strategies and herbivore tolerance after two decades of climate change. *New Phytologist*, *235*(2), 773–785. https://doi.org/10.1111/nph.18125

Réale, D., McAdam, A. G., Boutin, S., & Berteaux, D. (2003). Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1515), 591–596. https://doi.org/10.1098/rspb.2002.2224

Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B.-E., & Visser, M. E. (2013). Population Growth in a Wild Bird Is Buffered Against Phenological Mismatch. *Science*, *340*(6131), 488–491. https://doi.org/10.1126/science.1232870

Reynes, L., Fouqueau, L., Aurelle, D., Mauger, S., Destombe, C., & Valero, M. (2024). Temporal genomics help in deciphering neutral and adaptive patterns in the contemporary evolution of kelp populations. *Journal of Evolutionary Biology*, *37*(6), 677–692. https://doi.org/10.1093/jeb/voae048

Rodríguez-Trelles, F., & Rodríguez, M. A. (1998). Rapid micro-evolution and loss of chromosomal diversity in Drosophila in response to climate warming. *Evolutionary Ecology*, *12*(7), 829–838. https://doi.org/10.1023/A:1006546616462

Rodríguez-Trelles, F., Tarrío, R., & Santos, M. (2013). Genome-wide evolutionary response to a heat wave in Drosophila. *Biology Letters*, *9*(4). https://doi.org/10.1098/rsbl.2013.0228

Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, *354*(6313). https://doi.org/10.1126/science.aaf7671

Simmonds, E. G., Cole, E. F., Sheldon, B. C., & Coulson, T. (2020). Testing the effect of quantitative genetic inheritance in structured models on projections of population dynamics. *Oikos*, *129*(4), 559–571. https://doi.org/10.1111/oik.06985

Spurlin, S. M., & Lambrecht, S. C. (2024). Rapid responses to drought in a rare California annual (San Francisco collinsia, Collinsia multicolor). *Plant Ecology*, *225*(9), 997–1007. https://doi.org/10.1007/s11258-024-01449-y

St. Lawrence, S., Blumstein, D. T., & Martin, J. G. A. (2023). The timing of reproduction is responding plastically, not genetically, to climate change in yellow-bellied marmots (Marmota flaviventer). *Ecology and Evolution*, *13*(12), 1–12. https://doi.org/10.1002/ece3.10780

Thomann, M., Imbert, E., Engstrand, R. C., & Cheptou, P. O. (2015). Contemporary evolution of plant reproductive strategies under global change is revealed by stored seeds. *Journal of Evolutionary Biology*, *28*(4), 766–778. https://doi.org/10.1111/jeb.12603

Thompson, J., Charpentier, A., Bouguet, G., Charmasson, F., Roset, S., Buatois, B., Vernet, P., & Gouyon, P. H. (2013). Evolution of a genetic polymorphism with climate change in a Mediterranean landscape. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(8), 2893–2897. https://doi.org/10.1073/pnas.1215833110

Turbek, S. P., Bossu, C., Rayne, C., Gruppi, C., Kus, B. E., Whitfield, M., Smith, T. B., Paxton, E. H., Bay, R. A., & Ruegg, K. C. (2023). Historical DNA reveals climate adaptation in an endangered songbird. *Nature Climate Change*, *13*(7), 735–741. https://doi.org/10.1038/s41558-023-01696-3

Umina, P. A., Weeks, A. R., Kearney, M. R., McKechnie, S. W., & Hoffmann, A. A. (2005). A rapid shift in a classic clinal pattern in Drosophila reflecting climate change. *Science*, *308*(5722), 691–693. https://doi.org/10.1126/science.1109523

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., … Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), 1113. https://doi.org/10.1126/science.aad8466

Urban, M. C., Swaegers, J., Stoks, R., Snook, R. R., Otto, S. P., Noble, D. W. A., Moiron, M., Hällfors, M. H., Gómez-Llano, M., Fior, S., Cote, J., Charmantier, A., Bestion, E., Berger, D., Baur, J., Alexander, J. M., Saastamoinen, M., Edelsparre, A. H., & Teplitsky, C. (2024). When and how can we predict adaptive responses to climate change? *Evolution Letters*, *8*(1), 172–187. https://doi.org/10.1093/evlett/qrad038

Vahsen, M. L., Kleiner, H. S., Kodak, H., Summers, J. L., Vahsen, W. L., Blum, M. J., Megonigal, J. P., & McLachlan, J. S. (2023). Complex eco-evolutionary responses of a foundational coastal marsh plant to global change. *New Phytologist*, *240*(5), 2121–2136. https://doi.org/10.1111/nph.19117

Valencia-Montoya, W. A., Flaven, E., Pouzadoux, J., Imbert, E., & Cheptou, P. O. (2021). Rapid divergent evolution of an annual plant across a latitudinal gradient revealed by seed resurrection. *Evolution*, *75*(11), 2759–2772. https://doi.org/10.1111/evo.14364

van Asch, M., Salis, L., Holleman, L. J. M., van Lith, B., & Visser, M. E. (2013). Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change*, *3*(3), 244–248. https://doi.org/10.1038/nclimate1717

van Asch, M., van Tienderen, P. H., Holleman, L. J. M., & Visser, M. E. (2007). Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biology*, *13*(8), 1596–1604. https://doi.org/10.1111/j.1365-2486.2007.01400.x

van Dis, N. E. (2025). Genetic adaptation to climate change in wild populations: a systematic literature review identifies opportunities to strengthen our evidence base. *Dryad*, *Dataset*. https://doi.org/10.5061/dryad.573n5tbh9

van Dis, N. E., Sieperda, G.-J., Bansal, V., van Lith, B., Wertheim, B., & Visser, M. E. (2023). Phenological mismatch affects individual fitness and population growth in the winter moth. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2005). https://doi.org/10.1098/rspb.2023.0414

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. B*, *275*, 649–659. https://doi.org/10.1098/rspb.2007.0997

Vtipil, E. E., & Sheth, S. N. (2020). A resurrection study reveals limited evolution of phenology in response to recent climate change across the geographic range of the scarlet monkeyflower. *Ecology and Evolution*, *10*(24), 14165–14177. https://doi.org/10.1002/ece3.7011

Waldvogel, A., Feldmeyer, B., Rolshausen, G., Exposito-Alonso, M., Rellstab, C., Kofler, R., Mock, T., Schmid, K., Schmitt, I., Bataillon, T., Savolainen, O., Bergland, A., Flatt, T., Guillaume, F., & Pfenninger, M. (2020). Evolutionary genomics can improve prediction of species' responses to climate change. *Evolution Letters*, *4*(1), 4–18. https://doi.org/10.1002/evl3.154

Welt, R. S., Litt, A., & Franks, S. J. (2015). Analysis of population genetic structure and gene flow in an annual plant before and after a rapid evolutionary response to drought. *AoB PLANTS*, *7*(1), 1–11. https://doi.org/10.1093/aobpla/plv026

Wooliver, R., Tittes, S. B., & Sheth, S. N. (2020). A resurrection study reveals limited evolution of thermal performance in response to recent climate change across the geographic range of the scarlet monkeyflower. *Evolution*, *74*(8), 1699–1710. https://doi.org/10.1111/evo.14041

Yang, Y., Sánchez-Tójar, A., O'Dea, R. E., Noble, D. W. A., Koricheva, J., Jennions, M. D., Parker, T. H., Lagisz, M., & Nakagawa, S. (2023). Publication bias impacts on effect size, statistical power, and magnitude (Type M) and sign (Type S) errors in ecology and evolutionary biology. *BMC Biology*, *21*(1), 71. https://doi.org/10.1186/s12915-022-01485-y

Yousey, A. M., Chowdhury, P. R., Biddinger, N., Shaw, J. H., Jeyasingh, P. D., & Weider, L. J. (2018). Resurrected 'ancient' Daphnia genotypes show reduced thermal stress tolerance compared to modern descendants. *Royal Society Open Science*, *5*(3). https://doi.org/10.1098/rsos.172193

Ziska, L. H. (2017). Could recent increases in atmospheric CO2 have acted as a selection factor in Avena fatua populations? A case study of cultivated and wild oat competition. *Weed Research*, *57*(6), 399–405. https://doi.org/10.1111/wre.12271

Zivanovic, G., Arenas, C., & Mestres, F. (2015). Medium-term changes in Drosophila subobscura chromosomal inversion polymorphism: a possible relation with global warming? *Journal of Genetics*, *94*(2), 343–346. https://doi.org/10.1007/s12041-015-0523-z

Zivanovic, G., Arenas, C., & Mestres, F. (2019). Rate of change for the thermal adapted inversions in Drosophila subobscura. *Genetica*, *147*(5–6), 401–409. https://doi.org/10.1007/s10709-019-00078-y