Genetic adaptation of wild populations under climate change: building up the evidence base

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Running Head: Existing evidence for climate change adaptation

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Abstract

To understand to what extent evolution can contribute to bending the curve of ongoing biodiversity losses, we urgently need to characterize the rate of genetic adaptation in wild populations. However, we lack a comprehensive overview of which species and populations have been tested to date and the strength of evidence these studies provide. In this review, I systematically assessed the evidence of genetic adaptation to climate change on four criteria that together robustly demonstrate that genetic changes are adaptive and driven by climate change. I determined whether strong inference methods were used to (1) test for genetic change over time, (2) show that the observed genetic change is associated with climate change, (3) establish that the fitness of the phenotype / genotype depends on the climatic variable that changed over time, and (4) assess population genetic continuity over time to rule out purely neutral evolution. I identified 44 species that were tested for genetic change under climate change using strong inference methods, with a number of patterns emerging from this overview. The 44 species tested were mostly from the terrestrial realm in temperate regions and encompassed eight higher taxa (16 plants, 7 insects, 7 birds, 5 mammals, 4 fish, 2 crustaceans, 2 molluscs, and 1 alga), with 39 species having evidence that genetic change had occurred in wild populations and 5 species evidence that no genetic change occurred albeit for 4 of these 5 species only one population has been tested so far. In fact, climate change responses were highly population specific, with clear variation within species (152 of the 253 populations tested were found to have genetically changed over time). Finally, in most species, responses to climate change were associated with changes in temperature and/or precipitation, where climate change was found to have both direct effects on survival and reproduction as well as indirect effects through changing species interactions. However, with regard to the strength of evidence, only 3 out of the 44 tested species met the criteria for demonstrating that the observed genetic responses are indeed adaptive and driven by climate change. I urge the field to strengthen the

evidence base of genetic adaptation to climate change in wild populations as this is needed before it is possible to draw robust conclusions about the role of genetic adaptation in population persistence. In addition, testing more species to improve taxonomic and geographic representation as well as increasing spatial and temporal replication per species would allow for the exciting opportunity to start empirically testing drivers and constraints that determine the 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 genetic adaptation 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). Genetic adaptation is the evolutionary process where the genetic composition of the population changes in response to natural selection leading to an increase in the average fitness of the population over time. For effective conservation, we thus need to know what determines a population's adaptive potential to be able to predict species' responses to climate change (Eizaguirre & Baltazar-Soares, 2014; Urban et al., 2016). A large variety of approaches are 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, it is critical that we also test whether genetic adaptation is occurring in wild 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). Whether genetic adaptation is occurring in wild populations can be inferred both at the phenotype and genotype level, but convincingly demonstrating genetic adaptation requires robust inference methods (Merilä & Hendry, 2014). I provide an overview of which methods are used in the field and the strength of evidence they provide in Methods section 2.1 below, but ultimately, evidence over a period of multiple generations is needed to convincingly show genetic adaptation to climate change. Such temporal data allow for the 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 of the phenotype under selection (Franks & Hoffmann, 2012; Merilä & Hendry, 2014; Urban et al., 2024).

Importantly, while sampling a population at two timepoints (i.e. before and after environmental change) might already allow for observing genetic change, a key problem with just two time points is that it can lead to erroneous conclusions. As not only selection, but also genetic drift and gene flow can result in changes in the genomic composition of a population, it is more difficult to distinguish between random genetic change and adaptive genetic change with just two timepoints (Clark et al., 2023). Moreover, when comparing just two years, these years can differ in many different aspects in addition to climate change, making it very hard to provide convincing evidence that climate change is driving the observed genetic changes (Reinke et al., 2019). 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 the likelihood and rate of genetic adaptation to climate change, there are calls to initiate long-term monitoring programs to gain the temporal data needed to test for genetic adaptation 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 to date, including the strength of evidence these studies provide for genetic adaptation to climate change. Moreover, as temporal data take time to accumulate, it would be highly beneficial to meanwhile capitalise on existing examples of wild populations that have been tested for genetic adaptation to advance our knowledge of 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, as part of a special issue that reviewed the strength of support of different inference approaches (Merilä & Hendry, 2014) and then used this assessment to review the evidence for genetic adaptation to climate change in birds (Charmantier & Gienapp, 2014), mammals (Boutin & Lane, 2014), fish (Crozier & Hutchings, 2014), amphibians and reptiles (Urban et al., 2014), terrestrial plants (Franks et al., 2014), marine plants and animals (Reusch, 2014), terrestrial arthropods (Schilthuizen & Kellermann, 2014), and freshwater invertebrates (Stoks et al., 2014).

The purpose of the current paper is to update the (Merilä & Hendry, 2014) special issue to obtain a comprehensive overview of which wild populations have been tested to date for genetic adaptation to climate change over time and to review the strength of evidence for each case study. 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 adaptation in invasive species, see (Kołodziejczyk et al., 2025)]. I start by outlining criteria for demonstrating genetic adaptation to climate change and their associated methods [following (Franks & Hoffmann, 2012; Hansen et al., 2012; Merilä & Hendry, 2014)], and then summarize and assess the evidence for adaptation in each identified study, paying particular attention to studies that collected data for more than two timepoints and for multiple populations. It is tempting to already perform a meta-analysis with the studies compiled here to draw conclusions about the role of genetic adaptation in population persistence under climate change. While the overview of studies I present is a preparatory step in that direction, I will show that the evidence is not yet complete enough to draw robust conclusions. This paper is thus not a meta-analysis, but a call to action to strengthen our evidence base. I discuss how the field has progressed in the last decade, identify patterns that seem to be emerging from the data, and highlight important gaps in our evidence base, using case studies to illustrate why we need robust inference to fill these gaps. This review will allow the field to better utilize and build on the existing evidence of genetic responses to climate change to improve the predictability of adaptation to climate change in wild populations.

2. Methods

2.1 Criteria for demonstrating genetic adaptation driven by climate change

To assess the evidence for genetic adaptation to climate change, 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 four 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 (criterion 1). To assess whether an observed genetic change is indeed driven by climate change, it is furthermore necessary to establish that the observed genetic change is associated with climate change (criterion 2). In this regard, an environmental assessment is important to establish that the population has been subjected to climate change during the time period tested, with the strongest evidence provided when that climate change trend is linked to evidence showing a change in selection on the population in the same time period. For example in the case of short-term climate fluctuations, while such fluctuations can induce bouts of strong selection that can lead to rapid genetic change (e.g. response to a cold snap in green anole lizard populations, (Campbell-Staton et al., 2017), it is important to establish whether these climate fluctuations are in line with the climate change trend that the population has experienced (e.g. test whether climate change has involved an increase in the frequency of cold snaps in that region). Third, studies need to establish climate causality and show that the observed genetic change is adaptive by providing evidence that the fitness of the phenotype or genotype showing the temporal change depends on the climatic variable that has changed over time – either directly or indirectly (criterion 3; as opposed to genetic adaptation occurring solely in response to other selection pressures). For example, shifts in the clinal patterns of *Drosophila subobscura* inversion polymorphisms strongly correlated with warming trends (e.g. (Rodríguez-Trelles & Tarrío, 2024), but without knowing whether the genotypes that have increased in frequency also have higher fitness when exposed to warmer temperatures, we cannot be confident that the observed genetic shifts are an adaptation to climate change (discussed in more depth below). I consider selection from climate change to be direct when there is a direct link between the climate variable that changed over time and fitness, for example in the case of thermal tolerance traits, when an increase in temperature would push individuals beyond their thermal limit and would consequently cause increased mortality rates and/or decreased reproductive output

(Diamond, 2017). Selection can be considered indirect when fitness is impacted by climate change via other changes in the environment, for example in the case of phenology traits, when an increase in temperature advances the timing of resources and a population's phenology relative to the timing of those resources determines survival and/or reproduction (Visser & Gienapp, 2019). Finally, studies need to provide evidence of population continuity to rule out that the observed genetic changes are solely driven by evolutionary processes other than selection (i.e. gene flow, spatial sorting and genetic drift; criterion 4). While in essence, each process can lead to adaptive genetic change in the population, genetic change that is mainly driven by genetic drift or gene flow leading to population replacement would lead to very different conclusions about what determines a population's adaptative potential under climate change (Hansen et al., 2012).

To assess the strength of evidence for genetic adaptation to climate change, I assessed for each criterion whether studies used strong or only supportive inference methods [following (Hansen et al., 2012; Merilä & Hendry, 2014)]. Table 1 lists the four assessment criteria including the methods that provide strong vs supporting evidence for each criterion [for an in-depth discussion of why these methods are strong or only supporting, see (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 criterion 1: animal model, see Table 1) underlying the progressive advancement of parturition date observed in the population, finding that the population genetically changed over time. Evidence that this change is adaptive and driven by climate change comes from the fact that the onset of the plant growing season (the red deer's food source) also advanced over time due to a significant increase in the number of growing degree days (environmental assessment) and that females with earlier parturition dates had higher lifetime breeding success [supporting

evidence criterion 2: temporal trend in local climate in the same time period and population changed in expected direction, (Moyes et al., 2011)]. However, aside from the fact that a higher number of growing degree days tended to advance parturition date and females with earlier parturition dates had higher fitness, the fitness of the phenotype has not yet been experimentally linked to this climatic variable (evidence is correlational not causal, supporting evidence criterion 3: phenotypic selection estimates). 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 criterion 4: animal model).

Table 1. Criteria and 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 criterion was assessed by determining whether the listed strong methods vs supporting methods were used for inference (see main text for an assessment example). For each listed method, the reader is referred to a case study summarized in Table S2 for an example.

Criterion (1)	Test for genetic change over time in the population, ideally linked to the phenotype / genotype under selection (see criteria 2-3 below).
<u>Strong evidence</u>:	• Genotypes: molecular genetic approaches (i.e. test whether the allele frequency of genetic markers has changed over time) *Example: Drosophila robusta* • Phenotypes: repeated common-garden experiments or resurrection experiments (Franks et al., 2018), combined with evidence for trait heritability (i.e. accounting for maternal and storage effects) *Examples: yellow dung fly (Scathophaga stercoraria) [repeated common garden experiment], field mustard (Brassica rapa) [resurrection experiment]* • Phenotypes: repeated field observations of traits with a strong genetic basis (e.g. colour polymorphisms) *Example: land snail Cepaea hortensis* • Phenotypes: animal model [i.e. mixed model incorporating multigenerational / pedigree information to statistically estimate genetic parameters (Kruuk, 2004)] *Example: collared flycatcher (Ficedula albicollis)*

Supporting evidence:	• Phenotypes: comparison to model predictions *Example: sockeye salmon (Oncorhynchus nerka)*
Criterion (2)	Show that the observed genetic change is associated with climate change.
Strong evidence:	• demonstrate a temporal association between phenotypic / genotypic selection estimates and local climate change *Example: snow vole (Chionomys nivalis)*
Supporting evidence:	• temporal trend in local climate in the same time period *Example: cold-water kelp Laminaria digitata* • based on evidence for criterion 3 (see below), population changed in the expected direction (more convincing with many timepoints / populations) *Example: pitcher-plant mosquito (Wyeomyia smithii)*
Criterion (3)	Provide evidence that the fitness of the phenotype / genotype depends on the climatic variable that changed over time (identified in criterion 2).
Strong evidence:	• experimental evolution *Example: water flea Daphnia magna* • reciprocal transplants in the field or lab *Example: cutleaf monkeyflower (Mimulus laciniatus) [field], winter moth (Operophtera brumata) [lab]*
Supporting evidence:	• phenotypic / genotypic selection estimates *Example: blue tit (Cyanistes caeruleus)* • space-for-time substitutions (i.e. phenotype / genotype varies consistently with geographic climatic variation) *Example: threespine stickleback (Gasterosteus aculeatus)*
Criterion (4)	Assess population genetic continuity over time to rule out purely neutral evolution (e.g. genetic drift or simple replacement where the original population has been replaced by another population) as opposed to a response to selection.
Strong evidence:	• molecular genetic approaches *Example: Arabidopsis thaliana* • animal model *Example: red deer (Cervus elaphus)* • absolute population tracking (e.g. in a closed lake) *Example: Soay sheep (Ovis aries)*
Supporting evidence:	• assess likelihood of genetic drift and/or migration *Example: red squirrel (Tamiasciurus hudsonicus) [genetic drift], wild thyme (Thymus vulgaris) [likelihood of migration]*

2.2 Systematic literature review

To gather species with wild populations that have been tested for 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' [1347 records, accessed on 2026-02-02]. 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 45 records to read in-depth, summarizing and assessing whether the four 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') [1190 records in WoS categories 'Ecology' and 'Evolutionary Biology', accessed on 2026-02-02], leading to an additional 12 records selected for assessment (Table S2). Finally, I assessed an additional 65 papers that came to my attention while selecting and assessing the WoS records [e.g. examples identified in previous literature reviews (Merilä & Hendry, 2014; Scheffers et al., 2016) and examples or evidence cited by assessed studies, Table S2]. Studies were only included in the final overview presented below when they had at least tested for

genetic change over time using a strong inference method (criterion 1) and provided either strong or supportive evidence to establish whether the population was under selection from climate change in the same time period (criterion 2, see Table 1).

3. Results and Discussion

3.1 Overview and emerging patterns

Taxonomic and geographic representation

The systematic literature review identified 44 empirical examples of species with wild populations that were tested for genetic change in response to climate change using strong inference methods (Table 2, with the underlying evidence extracted from 73 published papers). Together, these 44 species encompassed eight higher taxa (Fig.1; 16 plants, 7 insects, 7 birds, 5 mammals, 4 fish, 2 crustaceans, 2 molluscs, and 1 alga). Fungi, amphibians, reptiles, arthropods other than insects, 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=37 species). To increase geographic representation in the future, more studies on fresh-water species (currently N=3), marine species (currently N=4), tropical species (currently N=1), and polar species (currently N=1) are needed.

Table 2. Evidence of genetic adaptation driven by climate change. The systematic literature review identified 44 species, from eight higher taxa, with wild populations that have been tested for genetic adaptation to climate change over time. For each species, I noted which trait was studied and whether genetic change was detected yes (Y) or no (N), and then assessed whether strong (++), only supporting (+-), or no (--) evidence was provided for the four criteria that demonstrate that a wild population is genetically adapting to climate change (Table 1). For each study system, it is also noted which climate variable imposed selection on the population; whether expression of the trait depends on a climatic variable (i.e. climate plasticity); how many timepoints were studied and how many populations, and for how many of those populations genetic change was observed; 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 three criteria [light grey] or all four assessment criteria [dark grey]. Studies highlighted in orange found no genetic change over time. Cells highlighted in green note studies with at least three timepoints and/or populations.

				Strength of evidence											
Taxa	**Species**	**Trait**	**Genetic change detected?**	**(1) Genetic change?**	**(2) Climate change?**	**(3) Fitness climate dependent?**	**(4) Population genetic continuity?**	**Selection type?**	**Climate plastic trait?**	**# Timepoints**	**# Populations**	**#Pop that changed**	**Genomic data?**	**Data available?**	**Refs**
alga 	*cold-water kelp *Laminaria digitata*	(allele frequency)	Y	++	+-	+-	++	🌡	?	2	3	2	Y	Y	(Reynes et al., 2024)
bird 	black cap (*Sylvia atricapilla*)	Phenology	Y	++	+-	--	--	🌡	?	13	1	1			(Pulido & Berthold, 2010)
	*blue tit (*Cyanistes caeruleus*)	Phenology	N	++	++	+-	--	🌡	P	44	1	0		Y	(Biquet et al., 2022; Bonamour et al., 2019)
	collared flycatcher (*Ficedula albicollis*)	Colouration; Phenology	Y	++	++	+-	+-	🌡	P	34	1	1		p	(Brommer et al., 2005; Evans & Gustafsson, 2017)
	*common tern (*Sterna hirundo*)	Phenology	Y?	++	++	+-	+-	🌡	P	27	1	1?		Y	(Moiron et al., 2024)
	great tit (*Parus major*)	Phenology	N	++	++	+-	--	🌡	P	44	1	0		Y	(Gienapp et al., 2006; Ramakers et al., 2019)

Taxa	Species	Trait	Genetic change detected?	(1) Genetic change?	(2) Climate change?	(3) Fitness climate dependent?	(4) Population genetic continuity?	Selection type?	Climate plastic trait?	# Timepoints	# Populations	#Pop that changed	Genomic data?	Data available?	Refs
bird 	*southwestern willow flycatcher (*Empidonax traillii extimus*)	(allele frequency)	Y	++	+-	+-	++		?	2	1	1	Y	Y	(Turbek et al., 2023)
	tawny owl (*Strix aluco*)	Colouration	Y	++	++	+-	+-		NP	28	1	1			(Karell et al., 2011; Koskenpato et al., 2023)
crustacean 	*water flea *Daphnia magna*	Thermal tolerance	Y	++	+-	++	++		?	2	1	1	Y		(Geerts et al., 2015; Jansen et al., 2017)
	*water flea *Daphnia pulicaria*	Thermal tolerance	Y	++	+-	--	++		?	2	1	1		Y	(Karapli-Petritsopoulou et al., 2025)
fish 	*Atlantic killifish *Fundulus heteroclitus*	(allele frequency) / Thermal tolerance?	N	++	+-	+-	+-		?	2	13	1		Y	(Bell et al., 2014)
	*Atlantic salmon (*Salmo salar L.*)	Growth	Y	++	+-	+-	++		P	25	1	1	Y	Y	(Besnier et al., 2024)
	pink salmon (*Oncorhynchus gorbuscha*)	Phenology	Y	++	+-	--	+-		?	7	1	1		Y	(Kovach et al., 2012)
	*threespine stickleback (*Gasterosteus aculeatus*)	Morphology	Y	++	+-	+-	--		NP	4	2	1		Y	(Des Roches et al., 2020)
insect 	*Drosophila melanogaster*	(allele frequency)	Y	++	+-	+-	--		?	2	1	?			(Anderson et al., 2005; Umina et al., 2005)
	Drosophila robusta	(allele frequency)	Y	++	+-	+-	+-		?	19	2	2		p	(Etges & Levitan, 2008; Levitan & Etges, 2005)
	Drosophila subobscura	(allele frequency) / Thermal tolerance?	Y	++	+-	+-	++		?	9	29	27		p	(Balanya et al., 2006; Rodríguez-Trelles et al., 2013; Rodríguez-Trelles & Rodríguez, 1998; Rodríguez-Trelles &

															Tarrío, 2024; Zivanovic et al., 2015, 2019, 2025a, 2025b)

Taxa	Species	Trait	Genetic change detected?	(1) Genetic change?	(2) Climate change?	(3) Fitness climate dependent?	(4) Population genetic continuity?	Selection type?	Climate plastic trait?	# Timepoints	# Populations	#Pop that changed	Genomic data?	Data available?	Refs
insect 	pitcher-plant mosquito (*Wyeomyia smithii*)	Phenology	Y	++	+-	+-	--	🌡	?	2	31	8			(Bradshaw & Holzapfel, 2001)
	two-spot ladybird (*Adalia bipunctata*)	Colouration	Y	++	+-	+-	--	🌡	NP	5	16	9		p	(Brakefield & De Jong, 2011)
	*winter moth (*Operophtera brumata*)	Phenology	Y	++	++	++	--	🌡	P	16	3	3			(van Asch et al., 2013)
	*yellow dung fly (*Scathophaga stercoraria*)	Body size	Y	++	+-	+-	--	🌡	P	12	1	1		Y	(Blanckenhorn, 2015)
mammal 	*alpine chipmunk (*Tamias alpinus*)	(allele frequency) / Physiology?	Y	++	+-	--	++	🌡	?	2	2	1	Y	Y	(Bi et al., 2019)
	*lodgepole chipmunk (*Tamias speciosus*)	(allele frequency)	N	++	+-	--	++	🌡	?	2	1	0	Y	Y	(Bi et al., 2019)
	*red deer (*Cervus elaphus*)	Phenology	Y	++	+-	+-	++	🌡	P	45	1	1		Y	(Bonnet et al., 2019)
	red squirrel (*Tamiasciurus hudsonicus*)	Phenology	N	++	+-	--	+-	-	NP	19	1	0			(Lane et al., 2018)
	*snow vole (*Chionomys nivalis*)	Body size	Y	++	++	+-	++	🌡🌧	P	9	1	1		Y	(Bonnet et al., 2017)
mollusc 	brown-lipped banded snail (*Cepaea nemoralis*)	Colouration	Y	++	+-	+-	--	🌡	NP	6	60	36		p	(Cameron & Cook, 2013; Cowie & Jones, 1998; Ożgo & Schilthuizen, 2012)

Taxa	Species	Trait	Genetic change detected?	(1) Genetic change?	(2) Climate change?	(3) Fitness climate dependent?	(4) Population genetic continuity?	Selection type?	Climate plastic trait?	# Timepoints	# Populations	#Pop that changed	Genomic data?	Data available?	Refs
mollusc	land snail *Cepaea hortensis*	Colouration	Y	++	+-	+-	--		NP	3	16	11		p	(Cameron & Pokryszko, 2008; Cowie & Jones, 1998)
plant	**Arabidopsis thaliana*	Phenology; Growth; Morphology	Y	++	+-	+-	++		?	2	1	1	Y	Y	(Frachon et al., 2017)
	**Clarkia xantiana*	Phenology	Y	++	+-	++	+-		?	3	2	1		Y	(Benning et al., 2023)
	**Clinopodium vulgare*	Growth; Phenology	Y	++	+-	+-	++		P	2	1	1		Y	(Karitter et al., 2024; Rauschkolb, Henres, et al., 2022; Rauschkolb, Li, et al., 2022)
	*cornflower (*Cyanus segetum*)	Phenology	Y	++	+-	+-	++		?	3	3	3		Y	(Thomann et al., 2015; Valencia-Montoya et al., 2021)
	*cutleaf monkeyflower (*Mimulus laciniatus*)	Phenology	Y	++	+-	++	+-		?	2	1	?		Y	(Dickman et al., 2019)
	*European beech (*Fagus sylvatica*)	(allele frequency)	Y	++	+-	+-	+-		?	4	3	2	Y		(Jump et al., 2006)
	field mustard (*Brassica rapa*)	Phenology; Growth; Physiology	Y	++	++	++	++		P	4	2	2	Y	p	(Franks et al., 2007, 2016; Hamann et al., 2018; Welt et al., 2015)
	**Leontodon hispidus*	Growth; Phenology	Y	++	+-	+-	++		P	2	1	1		Y	(Karitter et al., 2024; Rauschkolb, Henres, et al., 2022; Rauschkolb, Li, et al., 2022)
	**Matthiola tricuspidata*	Growth; Phenology	Y	++	+-	--	++		P	2	1	1		Y	(Rauschkolb, Li, et al., 2022)

Taxa	Species	Trait	Genetic change detected?	(1) Genetic change?	(2) Climate change?	(3) Fitness climate dependent?	(4) Population genetic continuity?	Selection type?	Climate plastic trait?	# Timepoints	# Populations	#Pop that changed	Genomic data?	Data available?	Refs
plant	**Plantago crassifolia*	Growth; Physiology	Y	++	+-	--	++	drought	P	2	1	1		Y	(Rauschkolb, Li, et al., 2022)
	*San Francisco collinsia (*Collinsia multicolor*)	Phenology; Morphology	Y	++	+-	+-	+-	drought	P	2	3	2			(Spurlin & Lambrecht, 2024)
	*scarlet monkeyflower (*Mimulus cardinalis*)	Thermal tolerance; Phenology; Growth; Physiology	Y	++	++	+-	--	temperature; drought	P	7	11	3	Y	p	(Anstett et al., 2021, 2026; Sheth et al., 2026; Waits et al., 2025; Wilborn-Pilotte et al., 2025; Wooliver et al., 2020)
	*true babystars (*Leptosiphon bicolor*)	Phenology; Morphology	Y	++	+-	+-	--	drought	P	2	3	3		Y	(Lambrecht et al., 2020)
	*wild oat (*Avena fatua*)	Growth	Y	++	+-	--	--	CO2	P	2	1	1			(Ziska, 2017)
	*wild pansy (*Viola arvensis*)	Phenology; Colouration; Morphology	Y	++	+-	--	--	temperature	?	2	1	1		Y	(Cheptou et al., 2022)
	wild thyme (*Thymus vulgaris*)	Physiology	Y	++	++	++	+-	temperature	NP	2	24	17			(Thompson et al., 2013)

Notes on table legend:

- * = Study systems newly identified compared to the last systematic literature review on wild populations genetically adapting to climate change, performed more than a decade ago [N=29 new since special issue (Merilä & Hendry, 2014) and references therein].
- P = climate plastic, NP = not climate plastic, ? = no evidence provided or evidence is uncertain, 'p' = only partly/processed data available.
- The type of selection pressure imposed by climate change investigated is indicated with icons: temperature; / =precipitation [rain/snow]; = drought; =CO2; =inundation & salinity; =extreme event; - = no selection from climate change detected.
- See Table S2 for a summary of the evidence from the underlying papers assessed per species (cited here under Refs).
- Taxa pictures were freely available in the public domain and obtained via https://www.phylopic.org/.

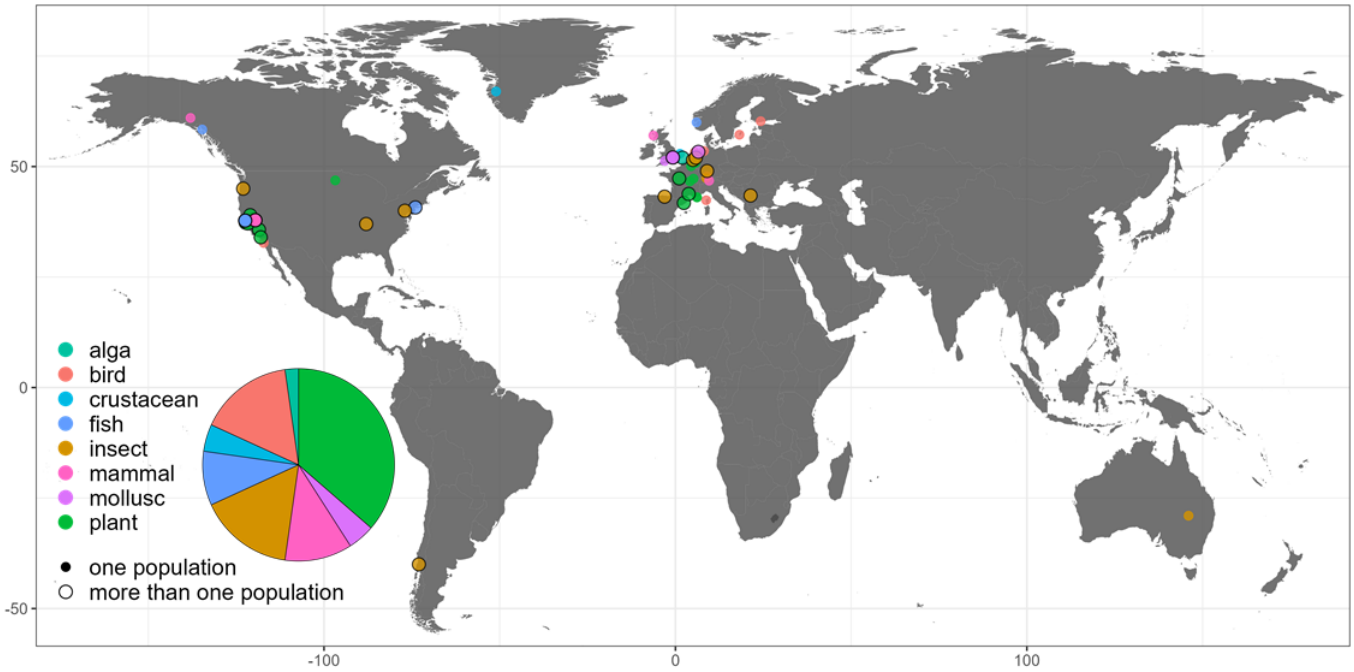


Figure 1. Taxonomic and geographic representation of evidence for genetic adaptation to climate change. The world map gives the spatial distribution of the 44 species with wild populations tested for genetic adaptation to climate change over time. Depicted are the locations of the studied species (latitude/longitude in decimals), with one point per published paper, coloured by taxa. The pie chart shows the proportion of species studied per taxon (16 plants, 7 insects, 7 birds, 5 mammals, 4 fish, 2 crustaceans, 2 molluscs, and 1 alga; of which no genetic change found for 2 birds, 2 mammals, and 1 fish [Table 2]).

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 same populations), while for one paper, three points were included: one for each cline studied on three different continents (total points depicted: N=52). Map base source: R Package "maps" v.3.4.3. Shapefile: Natural Earth https://www.naturalearthdata.com/about/terms-of-use/.

Frequency of genetic change: population-specific responses

Of the 44 identified study systems, 39 species had evidence that genetic change had occurred in wild populations, while for only 5 species virtually no populations were found to have genetically changed over time (Table 2, no genetic change found for 2 birds, 2 mammals, and 1 fish). But interestingly, for four of the five species for which no genetic change was found, only one population has been tested, while for species where multiple populations have been tested, responses often differed between populations (Table 2). Also note that we expect there to be a publication bias, where studies with negative results are less likely to be part of the publication record – 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 taking extra care to also publish null results, are crucial to validate the frequency of genetic adaptation in response to climate change. Furthermore, future use of meta-analysis approaches will be able to estimate the extent of publication bias against null results (Nakagawa et al., 2022).

Summing up across species, in total 253 populations have been effectively tested for genetic change, of which at least 152 were found to have genetically changed over time (Table 2 and Table S2). Taking into account the likely publication bias against null results, the 44 identified case studies cautiously suggest that in many cases where populations are tested for genetic change over time (criterion 1), genetic change is found. But these studies also show that there is a large set of populations for which genetic change was not observed. While these contrasting results could in part be due to methodological caveats (e.g. few genetic markers, low-powered statistical tests, missing traits, see Table S2), these studies strengthen the idea that responses to climate change are population specific, highlighting the need to study many populations to gain insight into what determines the rate of genetic adaptation to climate change. 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 (Brassica rapa: Franks et al., 2007; Leptosiphon bicolor: Lambrecht et al., 2020; Collinsia multicolor: Spurlin & Lambrecht, 2024), suggesting that population history is an important determinant of the rate of adaptation. The rate of adaptation could furthermore be influenced by fluctuating selection that could either constrain adaptation when net selection across the time period amounts to zero (Sæther & Engen, 2015) 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. Furthermore, continued long-term monitoring is needed to determine how this fluctuating selection influences the populations' long-term adaptative potential to climate change.

Genetic change vs plasticity

Phenotypes that have been tested for genetic change over time include phenology (N=22), growth (e.g. growth rate, reproductive biomass, plant size, N=9), colouration (N=6), morphology (N=5), physiology (e.g. water-use efficiency, stem diameter, N=4), thermal tolerance (N=3), and body size (N=2, Table 2); with some studies having only sampled genotypes (i.e. allele frequency shifts, N=9 of which N=3 having indications of which traits might be linked to these genotypes, Table 2). Note that several of the studies that found no genetic change did find phenotypic change over time (e.g. birds: *Cyanistes caeruleus*, *Parus major*), highlighting the significant contribution of plasticity 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=18 species, Table 2), with the few nonplastic phenotypes involving genetically determined colour morphs or ecotypes, or phenotypes that responded plastically to environmental variables other than those driven by climate (N=7, 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*: (van Asch et al., 2013), plants *Clinopodium vulgare*: (Karitter et al.,

2024), *Brassica rapa*: (Hamann et al., 2018), *Leptosiphon bicolor*: (Lambrecht et al., 2020); see Table S2). However, for a large portion of the studies, the climate plasticity of the studied phenotype or genotype remains unknown (N=19, Table 2), requiring follow-up studies to be able to investigate the relative contribution of plasticity and genetic change in determining population responses to climate change (Charmantier & Gienapp, 2014; Merilä & Hendry, 2014).

Selection pressures exerted by climate change

Changes in climate that populations experienced were most often reported to be changes in mean temperature (N=33 species), followed by precipitation (N=14, with the majority specifically dealing with periods of drought [N=11 of which N=10 in plants]), extreme temperature events (N=1), and CO2 levels (N=1); with only for one species (mammal: *Tamiasciurus hudsonicus*) no climate change observed in the climate variable that was thought to impose selection on the trait showing phenotypic change over time, which might explain the lack of a genetic response for the tested population (Lane et al., 2018), Table 2). While for most species, putative selection imposed by climate change thus seems to be related to temperature or precipitation, or both (N=5 species), studies that performed an in-depth characterization of how climate impacts fitness (i.e. with strong evidence for criterion 2 and/or 3, Table 2) indicate that climate change both impacted species directly and indirectly. For example, in wild Thyme (*Thymus vulgaris*) climate change led to a significant increase in winter temperatures such that freezing events are now above the mortality threshold of winter sensitive morphs (direct link between climate and fitness, strong evidence criterion 2 and 3: temporal association between phenotypic selection estimates and local climate change; reciprocal field and lab transplants), with this relaxed selection driving the observed increase of winter sensitive morphs in the populations (Thompson et al., 2013). Direct selection from climate change was similarly found for tawny owls (bird *Strix aluco* (Karell et al., 2011), snow voles (mammal *Chionomys nivalis*

(Bonnet et al., 2017), and plants: *Clarkia xantiana* (Benning et al., 2023), cutleaf monkeyflower (*Mimulus laciniatus* (Dickman et al., 2019), and field mustard (*Brassica rapa* (Hamann et al., 2018); Table S2). But changes in selection pressures due to climate change also frequently operated indirectly through changing species interactions – such as climate change impacting the phenological match between consumers and their food source (e.g. insect *Operophtera brumata*: (van Asch et al., 2013), mammal *Cervus elaphus*: (Bonnet et al., 2019), and birds *Cyanistes caeruleus*: (Biquet et al., 2022), *Parus major*: (Ramakers et al., 2019), Table 2 and S2).

All studies with strong evidence for criterion 2 and/or criterion 3 (Table 2) determined which phenotypes are affected by climate change and characterized the resulting fitness consequences, highlighting the value of phenotypic characterization for providing us with strong evidence on how climate change induces selection on populations. Moreover, phenotypic characterization allows for insights into what determines the rate of adaptation. For example, phenotypic characterization in the winter moth (insect *Operophtera brumata*) revealed that warming winters affected the extent of phenological mismatch between the timing of winter moth egg hatching and the timing of its food source, oak budburst, leading to increased selection for later hatching (strong evidence criterion 2: temporal association between phenotypic selection estimates and local climate change, (van Asch et al., 2007). Using a lab experiment, eggs were manipulated with temperature to hatch either before or after oak budburst, to show that phenological mismatch incurs strong fitness consequences, impacting the survival rates of freshly hatched caterpillars (strong evidence criterion 3: reciprocal lab transplants, (van Dis et al., 2023). These insights could be used to show that the winter moth has been under hard selection: winter moth abundances show cyclic population dynamics that are thought to be driven by density-dependent predator-prey relationships (Varley et al., 1973), but the individual fitness consequences of increased selection from climate change in recent years led to decreases

in winter moth population growth rates that exceeded the density-dependent growth rates (van Dis et al., 2023). Winter moths have rapidly genetically adapted in response to this selection (van Asch et al., 2013), while in contrast, the great tit (bird *Parus major*) that similarly experienced increased selection from climate change, has so far not genetically adapted [(Gienapp et al., 2006; Ramakers et al., 2019), Table 2)]. Phenotypic characterization in the great tit showed that, while the winter moth experienced hard selection, the great tit has so far only experienced soft selection: the fitness consequences of climate change in spring (reduced number of offspring due to mistiming with the peak of their food source, strong evidence criterion 2: temporal association between phenotypic selection estimates and local climate change) are buffered by population density-dependent survival in winter (Reed et al., 2013). These case studies suggest that the link between selection and population dynamics could be an important determinant of the rate of genetic adaptation, where hard selection (i.e. instances where selection impacts population growth rates) can induce rapid evolution.

3.2 Strengthening the evidence base

Slow but accumulating evidence

Whereas the last overview of evidence for genetic adaptation to climate change in wild populations reported that 28 species had been tested with 23 species found to have genetically changed over time [special issue led by (Merilä & Hendry, 2014)], the overview compiled here identified 44 species of which 29 species have been newly tested in the last decade (Table 2 and Figure 2), with 27 of these 29 newly tested species found to have genetically changed over time (note that because evidence for all species was reassessed here, some species included in the initial overview have not been included in the overview here, see Supplementary Tables). One reason for the increase in evidence is a surge in resurrection experiments that revive ancestors from dormant seeds or eggs and compare them to descendants sampled from the same population in a common environment to infer genetic change over time (strong method criterion

1; N=1 species from previous overview by (Merilä & Hendry, 2014), plus N=14 new species identified here, all plants or Daphnia). For the other half of the newly tested species, the methods used to strongly infer genetic change over time were molecular genetic approaches (N=5 from previous overview, plus N=11 new species), animal models (N=2 from previous overview, plus N=5 new species, all birds or mammals), repeated common garden experiments (N=2 from previous overview, plus N=2 new species, both insects), and repeated field observations for traits with a strong genetic basis (N=5 from previous overview, plus N=1 new fish species; Table S2), with some studies using more than one method.

Relative to the vast number of species and populations subjected to climate change (IPCC, 2022), 44 species for which genetic change has been strongly inferred is still relatively few (but see below for additional species with so far only supportive 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 at the phenotype level such as resurrection experiments, repeated experimentation, and individual tracking needed for applying animal models (i.e. strong methods criterion 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 whether populations are genetically changing in response to climate change, lending extra weight to the recent calls to initiate and maintain long-term monitoring of wild populations that would specifically allow for strongly inferring genetic change over time (Cocciardi et al., 2024; Jensen & Leigh, 2022; Urban et al., 2024).

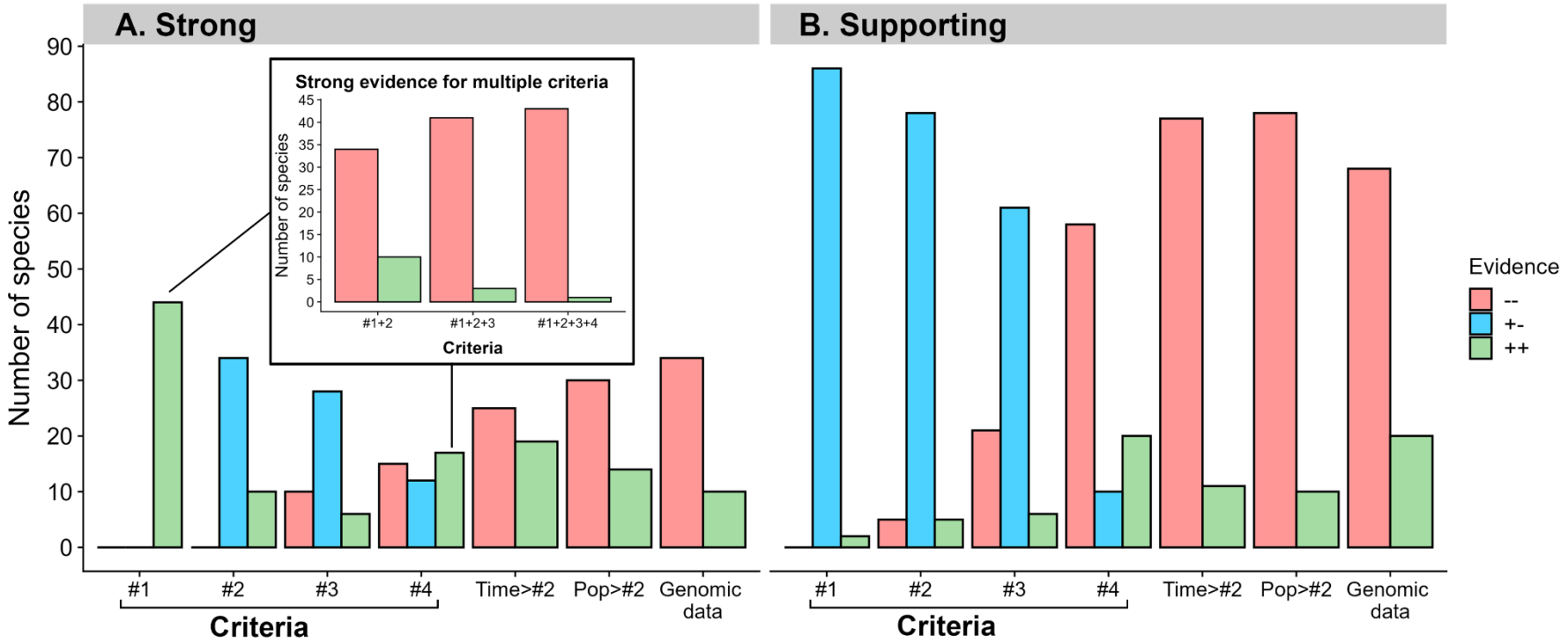


Figure 2. Evidence for genetic adaptation driven by climate change. Shown are the number of species that meet the criteria* to test whether a wild population has genetically adapted to climate change. **A)** Overview of species for which at least strong inference methods were used to test for genetic change over time (criterion 1: ++) and for which evidence has been provided for the role of climate change (criterion 2: ++ or +-), with the inset showing the number of studies that used strong inference methods for multiple criteria (see Table 1 and 2). **B)** Overview of species for which so far only supporting inference methods were used to test for genetic adaptation to climate change (criterion 1 and/or 2: +- or --, see Table 1 and S3). Species with sufficient temporal and spatial replication (i.e. at least 3 time points and populations sampled: ++) as well as species for which genomic data has been collected (++) present important opportunities to start validating what determines the rate of genetic adaptation to climate change in wild populations (see main text).

**Criteria: (1) Test for genetic change over time in the population, (2) Show that the observed genetic change is associated with climate change, (3) Provide evidence that the fitness of the phenotype / genotype depends on the climatic variable that changed over time, and (4) Assess population genetic continuity over time to rule out purely neutral evolution as opposed to a response to selection. Evidence: Red ('--') = no, not tested, Blue ('+-) = tested using supporting methods only, Green ('++') = yes, tested using strong inference methods (see Table 1).*

Promise of temporal genomics approaches

In the last decade, studies have started to use temporal genomics to assess genetic change under climate change but are still relatively few in number (Table 2 and Fig. 2A; N=10: 4 plants, 2 mammals, 1 alga, 1 bird, 1 crustacean, and 1 fish). The advent of applying genomics approaches to non-model species together with a reduction in sequencing costs opens the door to test for genetic changes in response to climate change in many more species (Clark et al., 2023; Waldvogel et al., 2020). Such temporal genomics approaches require sampling DNA of a representative number of individuals from a population at multiple time points and subsequently scanning the genome for regions whose allele frequencies have shifted over time (Clark et al., 2023). Sampling DNA can be done noninvasively, requires relatively few datapoints for strong inference (as opposed to data-intensive approaches such as animal models) and does not require prior knowledge about the phenotype under selection nor keeping individuals alive in experimental settings (e.g. prerequisites for criterion 1 strong inference approaches at the phenotype level, Table 1), which makes temporal genomics an ideal method for expanding the taxonomic and geographic representation of populations tested for genetic change over time.

Molecular genetic approaches, and particularly genomic data, have the added advantage that they can be used to estimate the extent of other evolutionary processes such as genetic drift and gene flow as opposed to selection driving genetic change in the population. In fact, for the majority of species, genomics might be the only feasible method that can be applied to strongly infer these evolutionary processes and so test for population genetic continuity over time (criterion 4), with absolute population tracking and data intensive animal models arguably less feasible for most species (Table 1). Indeed, to date, less than half of the studies have strongly inferred population genetic continuity over time (N=17, Fig. 2A and Table 2), with the vast majority of these having used molecular genetic approaches for strong inference (N=15),

followed by animal models (N=2) of which one study also used absolute population tracking (N=1). Because temporal genomics allows for estimating the relative contribution of different evolutionary processes, these studies could furthermore provide important insights into what determines the rate of adaptation. For example, the few genomics studies performed so far have provided important insights into the sources of genetic variation that selection from climate change can act on. So far only two studies have found 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 (Frachon et al., 2017; Reynes et al., 2024; Welt et al., 2015). Naturally, more studies are needed to confirm whether this is a general pattern. Interestingly, one of these studies also found that especially loci with an intermediate degree of pleiotropy showed the largest temporal differentiation indicating that the presence of variation at such loci is an important factor determining the rate of evolution (Frachon et al., 2017), highlighting another promising use of temporal genomics: the possibility to look into the underlying genetic architecture of traits under selection.

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 populations (see above), it is crucial that such efforts are followed up by fitness characterizations and experimentation to establish whether genetic changes or the lack thereof are adaptive to climate change (criteria 2 and 3). Indeed, in addition to few species so far tested, the main reason why we cannot yet draw robust conclusions about the role of genetic adaptation in population persistence under climate change is that for the vast majority of the species tested, we lack strong evidence showing whether the observed genetic responses are adaptive and driven by climate change. Currently, very few studies have strong evidence for climate change

being the driver (criterion 2, N=10) or strong evidence that the fitness of the phenotype or genotype is indeed determined by climate (criterion 3, N=6; Fig. 2A), with only 3 out of 44 species having strong evidence for both these criteria to establish climate causality and the adaptive nature of the observed genetic changes (insect *Operophtera brumata*, and plants *Thymus vulgaris* and *Brassica rapa*, Table 2, case studies discussed in Section 3.1 above). So far, we can thus say that 39 species are genetically changing under climate change and 5 species not yet, but we can only be confident for three of these species that they are genetically adapting to climate change.

With only three examples that robustly tested for genetic adaptation to climate change, there are ample opportunities available for the other 41 species to further supplement their evidence base to corroborate that the observed genetic changes are indeed adaptive and driven by 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; Martin 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. 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

525 characterization, it is hard to say what is happening. What aspect of climate change is causally
526 driving the observed changes? Is it direct or indirect selection? Are the observed changes
527 adaptive and mainly driven by changes in standing variation in response to selection or are we
528 observing repeated range shifting? Indeed, some populations of *Drosophila subobscura* that
529 were tested for genetic continuity (criterion 4) do not show genetic continuity over time
530 (Zivanovic et al., 2025b). Answers to these questions are needed to be able to use these
531 examples for predicting population responses.

532 ### *Testing drivers and constraints of the rate of genetic adaptation*

533 Ultimately, the big question is not only whether genetic adaptation is occurring in wild
534 populations, but whether populations are able to adapt at a rate that allows them to keep up with
535 climate change to avoid population extinction (Gonzalez et al., 2013; Visser, 2008). There
536 exists a large body of research that has investigated population adaptive potential [reviewed in
537 (Martin et al., 2023) and (Urban et al., 2024)], for example using lab or field data to establish
538 whether there is genetic variation present in the population that selection could act on (e.g.
539 (Bonnet et al., 2022; Exposito-Alonso et al., 2019), experimental evolution (e.g. (Barton et al.,
540 2023), space-for-time substitutions (e.g. (Bay et al., 2018), and theoretical modelling (e.g.
541 (Chevin & Bridle, 2025). To understand to what extent these approaches can accurately predict
542 genetic adaptation to climate change, it is critical that we use the case studies that tested for
543 genetic adaptation in wild populations to validate what determines the rate of adaptation.
544 However, the majority of the 44 identified case studies did not yet discuss whether the rate of
545 genetic change is sufficient to keep up with climate change, let alone quantified that rate (not
546 yet discussed for N=26 species). Of the studies that did discuss the rate of genetic change, four
547 studies concluded that the observed rate matched the rate of climate change (Biquet et al., 2022;
548 Geerts et al., 2015; Rodríguez-Trelles & Tarrío, 2024; van Asch et al., 2013) and two studies
549 concluded that the current rate of change was too slow (Bi et al., 2019; Ramakers et al., 2019),

with the remaining studies being uncertain (N=11 species, see Table S2). For example, for a population of blue tits (*Cyanistes caeruleus*) that so far has not genetically changed over time (Table 2), both the tits and the peak of their food source has advanced in response to climate change, but they have done so at similar rates. As a result, the observed mismatch that leads to selection on the tits to advance their timing (strong evidence criterion 2: temporal association between phenotypic selection estimates and local climate change) has remained relatively small and stable over time, leading the authors to conclude that so far, phenotypic plasticity has allowed the population to track climate change (Biquet et al., 2022). In contrast, for the population tested of their sister species the great tit (*Parus major*), that is under the same selection pressure from climate change, the mismatch between the timing of the tits and the timing of their food source has increased over time, with their lack of response not matching the required shift to maintain fitness, leading the authors to conclude that genetic adaptation is going too slow (Ramakers et al., 2019).

While it is paramount that more follow up studies are conducted to assess and quantify whether the rate of genetic adaptation allows populations to keep up with climate change, the case studies discussed throughout this review suggest a range of factors that seem to influence the likelihood and rate of adaptation. These factors are in line with the adaptive potential literature (e.g. (Martin et al., 2023; Urban et al., 2024) and have been listed in Table 3, where most suggested factors are thought to both drive (e.g. large population size) or constrain (e.g. low population size) the rate of adaptation, depending on the context. Interestingly, while the adaptive potential literature suggests that phenotypic plasticity could either facilitate or hamper the rate of genetic adaptation (Chevin et al., 2010), plasticity has only been suggested as a constraint for the wild populations studied so far (Table 3). However, whether phenotypic plasticity impacts the rate of adaptation to climate change in wild populations and to what extent has not yet been empirically tested. In fact, so far only two of the 13 suggested drivers and

575 constraints have been empirically tested in wild populations to validate their role in determining
576 the rate of genetic adaptation: standing genetic variation (discussed in more depth below) and
577 pleiotropy (already discussed above). Moreover, several of the suggested factors such as
578 generation time and life history strategy would require a multispecies approach for validation,
579 emphasizing the need to broaden and strengthen the evidence base of genetic adaptation in wild
580 populations.

581 **Table 3. Possible drivers and constraints of the rate of adaptation suggested by evidence**
582 **from wild populations.** Listed are factors thought to have influenced the rate of genetic change
583 in the 44 species tested for genetic adaptation to climate change (Table 2), noting whether these
584 factors were thought to drive (+) or constrain (-) the rate of adaptation (see Table S2 for per
585 study breakdown), which studies suggested them, and whether these factors have been
586 empirically tested in wild populations to verify their impact.

Factor	Impact	Refs	Tested?
• amount of standing genetic variation present in the population for the phenotypes / genotypes under selection	+/-	15 species: (Benning et al., 2023; Bi et al., 2019; Bradshaw & Holzapfel, 2001; Des Roches et al., 2020; Dickman et al., 2019; Frachon et al., 2017; Geerts et al., 2015; Hamann et al., 2018; Jump et al., 2006; Kovach et al., 2012; Ramakers et al., 2019; Reynes et al., 2024; Rodríguez-Trelles & Tarrío, 2024; Turbek et al., 2023; Ziska, 2017)	Yes for one plant species (Anstett et al., 2026)
• assortative mating	+	2 species: (Benning et al., 2023; Moiron et al., 2024)	
• developmental constraints	-	1 species: (Hamann et al., 2018)	
• gene flow through space (e.g. migration, range shifting) and time (e.g. seed banks)	+/-	7 species: (Bi et al., 2019; Des Roches et al., 2020; Jump et al., 2006; Rodríguez-Trelles & Tarrío, 2024; Sheth et al., 2026; Thompson et al., 2013; Turbek et al., 2023)	Not yet, but potential constraining effect of seed banks corroborated with simulations for one plant species (Benning et al., 2023)
• genetic load	-	2 species: (Rodríguez-Trelles & Rodríguez, 1998; Valencia-Montoya et al., 2021)	

• genetic trait architecture / correlations / trade-offs / covariance (e.g. number of genes involved, epistasis, pleiotropy, heterozygote advantage, trait heritability)	+/-	17 species: (Anstett et al., 2021; Benning et al., 2023; Besnier et al., 2024; Biquet et al., 2022; Bonnet et al., 2017, 2019; Etges & Levitan, 2008; Hamann et al., 2018; Karell et al., 2011; Lambrecht et al., 2020; Lane et al., 2018; Ramakers et al., 2019; Rodríguez-Trelles & Rodríguez, 1998; Thomann et al., 2015; Thompson et al., 2013; van Dis et al., 2022; Zivanovic et al., 2025a)	Yes, pleiotropy tested for one plant species (Frachon et al., 2017)
• phenotypic plasticity	-	3 species: (Bell et al., 2014; Biquet et al., 2022; Lambrecht et al., 2020)	
• population size	+/-	3 species: (Reynes et al., 2024; Rodríguez-Trelles & Tarrío, 2024; Spurlin & Lambrecht, 2024)	
• preadaptation / population history	+/-	6 species: (Anstett et al., 2021; Etges & Levitan, 2008; Hamann et al., 2018; Lambrecht et al., 2020; Ramakers et al., 2019; Spurlin & Lambrecht, 2024)	
• selection type (e.g. hard vs soft, frequency-dependent, fluctuating through time and space)	+/-	16 species: (Branch et al., 2024; Cameron & Pokryszko, 2008; Cowie & Jones, 1998; Frachon et al., 2017; Hamann et al., 2018; Lane et al., 2018; Ożgo & Schilthuizen, 2012; Pulido & Berthold, 2010; Ramakers et al., 2019; Reynes et al., 2024; Rodríguez-Trelles & Rodríguez, 1998; Turbek et al., 2023; Valencia-Montoya et al., 2021; van Dis et al., 2023; Zivanovic et al., 2025a)	
• selection strength	+/-	14 species: (Anstett et al., 2021; Bell et al., 2014; Bi et al., 2019; Bonnet et al., 2017; Bradshaw & Holzapfel, 2001; Brakefield & De Jong, 2011; Cowie & Jones, 1998; Dickman et al., 2019; Hamann et al., 2018; Karapli-	

		Petritsopoulou et al., 2025; Rauschkolb, Li, et al., 2022; Rodríguez-Trelles & Tarrío, 2024; van Asch et al., 2013)	
• species characteristics (e.g. breadth of species range, generation time, life history strategies)	+/-	10 species: (Balanya et al., 2006; Benning et al., 2023; Cowie & Jones, 1998; Lane et al., 2018; Ramakers et al., 2019; Reynes et al., 2024; Sheth et al., 2026; van Asch et al., 2013; Ziska, 2017)	

587

588 ### *Improving spatial and temporal replication*

589 As outlined and exemplified in this review, sufficient temporal and spatial replication is needed
590 to (1) distinguish between selection and genetic drift, (2) to provide convincing evidence that
591 climate change is driving the observed genetic changes, and (3) to gain insights into what
592 determines population adaptive potential. Temporal and spatial replication for the identified 44
593 case studies is highly variable, with some studies having very high temporal (up to 45 years) or
594 spatial replication (up to 60 populations), but many studies having low replication levels (Table
595 2). Indeed, about half of the 44 case studies so far only sampled two timepoints (N=20) and
596 more than half of the studies assessed genetic adaptation to climate change in only one or two
597 populations (N=30), with very few species having both sufficient spatial and temporal
598 replication (N=8 with >2 timepoints and >2 populations, Fig. 2A, Table 2). With sufficient
599 temporal and spatial replication, the identified case studies present exciting opportunities to test
600 the drivers and constraints that are thought to determine the likelihood and rate of adaptation to
601 climate change in wild populations (Table 3). A very recent study by (Anstett et al., 2026)
602 exemplifies this power of replication. The authors used a space-for-time substitution approach
603 to identify which loci were associated with local climate across 55 wild populations of the
604 scarlet monkeyflower (*Mimulus cardinalis,* supporting evidence criterion 3). Space-for-time
605 substitutions operate under the major assumption that the genetic variation involved in local

adaptation across spatial climate gradients is the same variation that will be targeted across the species range by selection from climate change over time (Lovell et al., 2023). Due to the lack of long-term temporal data for many species, such space-for-time substitutions are frequently used to make predictions about population responses to future climate change [e.g. (Bay et al., 2018; Miller et al., 2020)]. (Anstett et al., 2026) performed a rare test of this assumption of space-time equivalence by subsequently sampling a subset of the 55 populations (N=11) at 7 timepoints, covering a period of extreme drought, to identify which of the space-for-time identified climate-associated loci changed over time more than what you would expect from genetic drift alone (strong evidence criterion 1: molecular genetic approach). Moreover, because the authors also collected demography data over time that they combined with the temporal genomics data, they were able to test the hypothesis that the level of standing genetic variation present in the population determines population recovery (strong evidence criterion 2: temporal association between genotypic selection estimates and local climate change). They found that genome-wide genetic diversity levels did not predict population growth during the drought, whereas genetic diversity levels at specifically climate-associated loci did correlate with the magnitude of population recovery. I urge the field to capitalize on and strengthen the existing evidence of genetic adaptation to climate change identified here (Table 2), allowing us to perform more such empirical tests to validate which factors determine the rate of genetic adaptation to climate change in wild populations (Table 3).

Low-hanging fruit to extend taxonomic and geographic representation

Like the previous review (Merilä & Hendry, 2014), this review has focused on studies that used strong inference methods to infer genetic change over time (criterion 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 test for genetic adaptation to climate change in wild populations over time (i.e. so far only supporting evidence

631 provided, Figure 2B, Table S2). These studies encompassed 84 additional species and
632 additional populations for 4 species already included in Table 2 (Table S3, 66 plants, 9 insects,
633 4 birds, 3 crustaceans, 2 mammals, 2 algae, 1 fish, 1 reptile; of which no indication of genetic
634 change for 16 of the 88 species: 12 plants, 2 birds, 2 mammals) and provide additional
635 suggestive evidence that genetic adaptation plays an important role in population responses to
636 climate change. With targeted follow-up studies to supplement their evidence base, these
637 supporting studies could greatly expand the taxonomic and geographic representation of
638 whether genetic adaptation is occurring in wild populations in response to climate change. The
639 lowest-hanging fruit are studies that used a repeated common-garden experiment or resurrection
640 experiment but that did not yet account for maternal (and storage) effects [N=66 additional
641 species, e.g. (Everingham et al., 2021; Helm et al., 2019; Higgins et al., 2014); Table S2]. I
642 recommend supplementing these studies with additional evidence for the genetic basis of the
643 trait, such as obtaining heritability estimates via breeding experiments or by utilizing genomic
644 data (Table 1), to strongly infer genetic change in response to climate change. For plants,
645 ecological and taxonomic representation can furthermore be easily extended through Project
646 Baseline: a USA seed bank collected in 2015 with good spatial replication (i.e. 10-20
647 populations sampled per species), specifically designed for resurrection experiments to assess
648 genetic adaptation over time [(Etterson et al., 2016), http://www.baselineseedbank.org/ at 65
649 species when last accessed on 2024-11-06)]. Similarly, species with populations for which
650 phenotypic and/or genotypic characterizations have already been performed at one time point,
651 such as space-for-time substitutions studies (Lovell et al., 2023), represent important
652 opportunities for resampling and testing for genetic change over time. Lastly, significant
653 opportunities exist for range shifting populations. Range shifting in response to climate change
654 is being observed for many species (Lenoir & Svenning, 2015; Parmesan & Yohe, 2003), but I
655 found only one study that sampled range shifting populations at more than one timepoint to

assess whether they genetically changed over time (range contracting populations of the mammal: *Tamias alpinus* (Bi et al., 2019), see Table 2). I thus highly recommend resampling range-shifting populations in the future to also investigate the role of genetic adaptation in these responses to climate change.

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 evolutionary responses, 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 the existing evidence of genetic adaptation to advance our knowledge of the drivers and constraints underlying the rate of adaptation to climate change (this review). To guide these efforts, this review compiled a comprehensive overview of which wild populations have been tested to date for genetic adaptation to climate change and assessed the strength of the evidence provided. In total, I identified 44 species that have been tested for genetic change in response to climate change using strong inference methods, encompassing eight higher taxa (Table 2). While taxonomic and geographic diversification is clearly needed in 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 genetic responses are often population specific and related to shifts in temperature and precipitation regimes, where climate change acts both through direct effects on survival and reproduction and indirect effects through changing species interactions. These studies furthermore suggest several factors that seem to influence the likelihood and rate of adaptation, including population history, fluctuating selection, the extent of population buffering (e.g. density-dependent population dynamics), and the level of standing genetic variation (Table 3).

By also assessing the strength of evidence for genetic adaptation to climate change in the 44 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 to further validate the frequency of genetic adaptation under climate change are the identified studies of an additional 84 species that used supportive but not yet strong methods for inferring genetic change under climate change (Table S3, Fig.2B). In this regard, temporal genomics is a promising method as it would allow for strong inference of genetic change over time in many more species and populations, with the added advantage that it is arguably the only feasible method for most species to strongly infer population genetic continuity over time. However, it is paramount that such efforts are followed up by phenotypic characterizations and experimentation, as so far, only for 3 of the 44 identified species it has been robustly demonstrated that the genetic change observed over time is in fact adaptive and driven by climate change (Table 2 and Fig.2A). Moreover, for the majority of the species tested so far, it has not yet been assessed whether the rate of genetic change is sufficient to keep up with climate change. These critical gaps in our evidence base are a call to action to conduct follow up studies for more species and use strong inference to identify the selection pressures and fitness consequences that climate change exerts, as such information is highly needed to accurately predict population responses (Garcia-Costoya et al., 2023; Martin 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=19 species without raw data, Table 2). 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 that underlie the likelihood and rate of genetic adaptation to climate change.

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 (currently only with reviewer access).

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