Genetic adaptation to climate change: a systematic literature review identifies opportunities to strengthen existing studies of wild populations

Natalie E. van Dis[1,2,3]*, Bregje Wertheim[2], and Marcel E. Visser[1,2]

[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

***Corresponding author:** Natalie E. van Dis, natalie.vandis@helsinki.fi

ORCID ID: 0000-0002-9934-6751

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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 what determines the adaptive potential of populations. We argue that capitalising on existing examples of genetic adaptation to climate change provides the opportunities to fill this major knowledge gap. We performed a systematic literature review and identified 40 empirical examples of species with direct evidence of wild populations undergoing genetic adaptation in response to climate change selection. Only two of these examples (crustacean *Daphnia magna* and plant *Brassica rapa*) presented robust evidence for genetic adaptation driven by climate change, using strong inference methods to show that (1) a phenotypic change over time occurred, (2) the phenotype has an additive genetic basis, (3) the fitness of the phenotype depends on a climatic variable, (4) climate change-induced selection occurred across generations, and (5) it was assessed to what extent the genetic change involved a response to selection compared to the contribution of other evolutionary processes. There thus are ample opportunities to strengthen the evidence base for these existing examples such that they can contribute to understanding when and how genetic adaptation to climate change takes place. Moreover, improving the spatial and temporal replication of these existing studies is needed to identify general principles across species and populations. Especially genomics studies using high-resolution temporal sampling provide important information about the process and rate of evolution, but the field currently lacks such high-resolution temporal genomics studies. We urge the field to capitalize on and strengthen these existing examples of genetic adaptation so that we can identify which drivers and constraints determine the likelihood and rate of evolutionary responses to climate change.

Lay summary

Climate change puts nature under immense pressure, with already hundreds of populations going extinct. To avoid extinction, populations need to evolve: they need to genetically adapt at a rate that allows them to keep up with the rate of climate change. However, we still know little about what determines a population's adaptive potential. Here, we performed a systematic literature review to gather examples of wild populations that have so far been able to genetically adapt to climate change. We found examples for 40 species encompassing nine high-level taxa (17 plants, 4 birds, 7 insects, 3 crustaceans, 3 mammals, 2 fish, 2 molluscs, 1 phytoplankton, and 1 reptile). However, only two species had strong evidence to show that they evolved under climate change, convincingly showing that (1) a phenotypic change over time occurred, (2) the phenotype has a genetic basis, (3) the fitness of the phenotype depends on a climatic variable, (4) climate change-induced selection occurred across generations, and (5) it was assessed to what extent the genetic change involved a response to selection compared to the contribution of other evolutionary processes. We call upon the research field of climate change adaptation to benefit from and further investigate these existing examples of genetic adaptation so that we can find out when and how genetic adaptation to climate change takes place. We identified three major opportunities for the field: (1) strengthen the evidence base for these existing examples such that they can contribute to our understanding of what determines a population's adaptive potential, (2) improve their spatial and temporal replication so that we can identify general principles across species and populations, and (3) perform genomics studies with many timepoints (i.e. high-resolution temporal genomics studies) to gain information about the process and rate of evolution under 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). However, we still know little about the drivers and constraints that determine the rate of genetic adaptation in the face of rapid global change (Capblancq et al., 2020; Franks & Hoffmann, 2012).

Ultimately, genetic data over a period of multiple generations are needed to convincingly show an evolutionary response to climate change. 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 trait under selection (Franks & Hoffmann, 2012; Merilä & Hendry, 2014; Urban et al., 2024). Population genomic analysis of temporal samples is an especially powerful method to investigate microevolution as it allows for distinguishing between different evolutionary processes that lead to genetic change over time [e.g. response to selection, migration, 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 adaptation, a key problem with just two time points is that it can lead to erroneous conclusions. Not only adaptation, but also drift and migration can result in differences in allele frequency over time, causing cumulative change 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)].

Current insights into the likelihood of evolutionary rescue during climate change mostly come from lab-based or model systems, for which it is difficult to say how applicable they are to natural populations (Urban et al., 2024). To improve the predictability of evolution, 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)]. As temporal data take time to accumulate, it would be highly beneficial to meanwhile capitalise on examples of natural populations for which genetic adaption to climate change has already been detected. However, the last systematic literature review on natural populations genetically adapting to climate change was performed a decade ago [(Merilä & Hendry, 2014) and references therein].

Here, we perform a systematic literature review to gather studies showing evidence of natural populations undergoing genetic adaptation in response to climate change selection. We start by outlining the criteria for convincingly showing 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. We 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 would provide highly needed opportunities to investigate the drivers and constraints that determine the likelihood and rate of adaptation to climate change 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? Do plastic and non-plastic traits evolve at different rates? And how does the likelihood of evolutionary rescue depend on the strength of selection, the level of standing genetic variation, and/or population dynamics? The key motivation for this review is to assess whether we have the data to start answering these pressing questions about the adaptive potential of wild populations, allowing the field to identify and strengthen existing examples of genetic adaptation to climate change to capitalise on.

2. Genetic adaptation driven by climate change

2.1 Criteria for robust evidence

To assess the evidence for genetic adaptation to climate change selection, we 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). To show convincingly that a wild population is genetically adapting to climate change, we used the following five criteria:

(1) Establish that the mean phenotype of a particular trait has changed in the population over time.

(2) Demonstrate that the phenotype has an additive genetic basis and is thus heritable.

(3) Provide evidence that the fitness of the phenotype depends on a climatic variable (e.g. experiments, latitudinal clines, field observations).

(4) Show that climate change-induced selection on the trait has occurred in the population across generations.

(5) Assess the relative contribution of adaptive and neutral evolutionary processes (i.e. response to selection vs. migration, spatial sorting, genetic drift).

For studies to meet these criteria, strong inferences are needed. To convincingly show that the observed phenotypic response reflects genetic changes (criteria 1 and 2), studies need to have used one of the following strong methods: animal models [i.e. mixed models incorporating multigenerational/pedigree information to statistically estimate genetic parameters (Kruuk, 2004)], common-garden experiments, and/or molecular genetic approaches [following (Merilä & Hendry, 2014)]. Furthermore, to convincingly show that the genetic change is an adaptive response to climate change-induced selection (criteria 3 and 4), studies need to show that climatic conditions have changed over time in addition to demonstrating a causal relationship between climate and the fitness of the phenotype using the following strong methods: reciprocal transplants or experimental studies (criteria 3), and experimental evolution or selection estimates [criteria 4, following (Merilä & Hendry, 2014)]. Finally, studies need to have assessed whether the observed genetic change involved a response to selection rather than being attributed to other evolutionary processes alone [criteria 5; e.g. genetic drift, migration, spatial sorting (Hansen et al., 2012)]. As such, providing robust evidence that a genetic change over time has occurred that is both adaptive and in response to climate change selection requires temporal data as well as in-depth knowledge about the trait under selection (Franks & Hoffmann, 2012; Merilä & Hendry, 2014).

2.2 Systematic literature review

To gather examples of genetic adaptation to climate change, we 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', 1201 records, accessed on 2024-10-23]. We first performed a selection round, reading all titles and abstracts, only selecting records that assessed genetic adaptation to climate change in wild populations over time (see Table S1). We selected 45 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 robust evidence of genetic adaptation in response to climate change. We 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). We furthermore assessed an additional 42 papers that came to our 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) or examples cited by assessed studies, Table S2]. Note that as our search terms are affirmative – specifically looking for populations in which genetic adaptation occurred – we as a result did not find many studies that assessed whether genetic adaptation had occurred but that did not find a genetic change over time (see Section 3.2 for discussion).

Importantly, we only included studies on adaptation to climate change in natural populations, thus excluding studies of invasive species adjusting to a new climate [e.g. (Krehenwinkel et al., 2015; Sultan et al., 2013; Urbanski et al., 2012)] or populations adjusting to other environmental changes [e.g. habitat fragmentation (Hill et al., 1999)]. Furthermore, studies were only included when they used a strong method to infer genetic change over time while accounting for maternal and storage effects [i.e. temporal data combined with animal models, common-garden experiments, or molecular genetic approaches (Merilä & Hendry, 2014)]. We thus only included studies that sampled at least two time points and that used a strong inference method to statistically test for a genetic change over time in response to climate change (34 papers of the 87 selected papers excluded, Table S2, but see Section 3.3 below).

3. Opportunities for highly needed empirical studies

3.1 Very few studies meet all criteria for robust evidence

In total, we identified 40 empirical examples of species with direct evidence of natural populations undergoing genetic adaptation in response to climate change selection (Table 1, from 53 published papers), encompassing a range of taxa (17 plants, 4 birds, 7 insects, 3 crustaceans, 3 mammals, 2 fish, 2 molluscs, 1 phytoplankton, and 1 reptile). Of these 40 species, 26 species were newly identified compared to the last systematic literature review on natural populations genetically adapting to climate change, performed a decade ago [(Merilä & Hendry, 2014) and references therein]. However, only two of the 40 identified examples show particularly robust evidence of natural populations genetically adapting to climate change (crustacean *Daphnia magna* and plant *Brassica rapa*, both resurrection experiments, Table 1). These studies use strong inference methods to demonstrate in wild populations that (1) a phenotypic change over time occurred, (2) the phenotype has an additive genetic basis, (3) the fitness of the phenotype depends on a climatic variable, (4) climate change-induced selection occurred across generations, and (5) it was assessed to what extent the genetic change involved a response to selection compared to the contribution of other evolutionary processes (see criteria outlined above). An additional three examples found robust evidence for criteria 1 to 4, but did

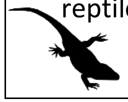
Table 1. Examples of genetic adaptation driven by climate change. We identified 40 examples of species, from nine higher taxa, with natural populations genetically adapting to climate change over time. For each species, we assessed whether strong evidence was provided for the five criteria that convincingly show that a wild population is genetically adapting to climate change (see main text). 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. 1A for a summary of the available evidence). Studies highlighted in grey show particularly convincing evidence of genetic adaption in response to climate change: they provide strong evidence for 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; 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) Temporal change in phenotype?	(2) Genetic basis?	(3) Fitness climate dependent?	(4) Climate change selection?	(5) Assessed which evolutionary processes?	Genomic data collected?	Data available?	Refs
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	n	**Y**	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**		n	Geerts et al., 2015
	*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	>=1	n	**Y**	*y*	*y* 🌡	n		n	Umina et al., 2005
	Drosophila robusta	(allele frequency)	?	18	22	n	**Y**	*y*	*y* 🌡	*y*		*p*	Etges & Levitan, 2008
	Drosophila subobscura	(allele frequency)	?	9	43	n	**Y**	**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	>=1	*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	>=1	**Y**	**Y**	**Y**	*y* 🌡	n		n	Cameron & Pokryszko, 2008; Cowie & Jones, 1998
	land snail *Cepaea nemoralis*	Coloration	NP	6	>=7	**Y**	**Y**	**Y**	*y* 🌡	*y*		*p*	Cameron & Cook, 2013; Cowie & Jones, 1998; Ożgo & Schilthuizen, 2012
	*spring bloom dinoflagellate *Apocalathium malmogiense*	Physiology	P	2	1	**Y**	**Y**	n	*y* 🌡	n		Y	Hinners et al., 2017

phyto-plankton													
plant	**Arabidopsis thaliana*	Phenology	P	2	1	**Y**	**Y**	*y*	*y* 🌡	**Y**	Y	Y	Frachon et al., 2017 but see (Gómez et al., 2018)
	**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	n	**Y**	*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
	*scarlet monkeyflower (*Mimulus cardinalis*)	Phenology; Physiology	P	7	3	*y*	**Y**	*y*	*y* 🌳	n		Y	Anstett et al., 2021 but see Vtipil & Sheth, 2020
	**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 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 a decade ago [N=26 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 we assessed per species (cited here under Refs).
- Taxa pictures were freely available in the public domain and obtained via https://www.phylopic.org/.

not quantify the contribution of other evolutionary processes (criterium 5; insect *Operophtera brumata*, plant *Clarkia xantiana* and plant *Thymus vulgaris*, Table 1).

The majority of the 40 included studies thus require follow-up studies using strong inference methods to supplement their evidence base and convincingly show genetic adaptation to climate change. A summary of the available evidence is provided in Figure 1A. While many studies investigated the phenotype under selection and linked the phenotype's fitness to climate (criteria 1 and 3, N=26), only 15 of these studies used strong inference methods for both criteria. Five studies did not investigate the phenotype under selection at all and only investigated genetic change and genetic correlations with climate (bird *Empidonax traillii extimus*, insects *Drosophila melanogaster*, *Drosophila robusta*, *Drosophila subobscura*, and plant *Fagus sylvatica*, Table 1). These study systems would benefit from follow-up studies focused on trait characterization, as in-depth knowledge about which traits experience the strongest selection combined with genotype-phenotype maps is expected to result in the most accurate predictions of populations responses to climate change (Garcia-Costoya et al., 2023; Urban et al., 2024). Indeed, such an in-depth trait characterization would give 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 (Franks & Hoffmann, 2012; Urban et al., 2023). For example, trait 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: climate change selection has been so strong that the fitness consequences of mistiming have negatively affected winter moth population growth rates, which could have been a driver of rapid adaptation (van Dis et al., 2023).

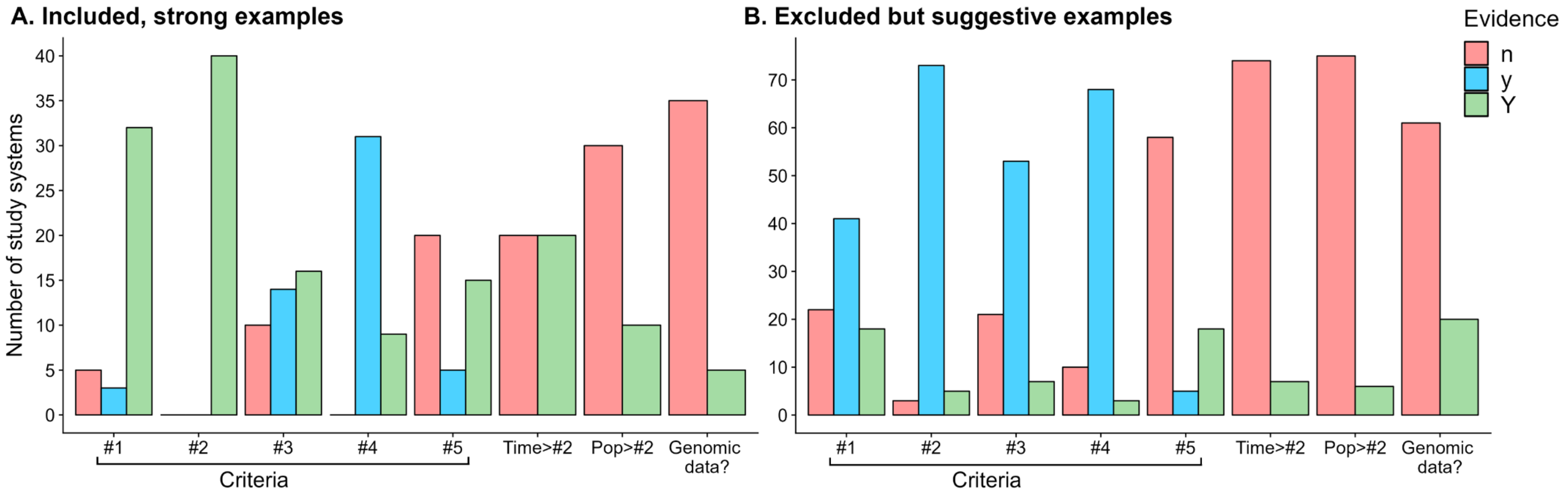


Figure 1. Evidence for genetic adaptation driven by climate change. Shown are the number of study systems that meet the criteria* to convincingly show that a wild population is genetically adapting to climate change for A) examples with strong inference of a genetic change over time [included in Table 1], and B) examples excluded due to the lack of strong inference but with suggestive evidence [Table S3, see Section 3.3 and Table S2 for details]. 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 the most highly needed opportunities to empirically test which drivers and constraints determine the likelihood and rate of evolutionary responses to climate change (see main text). Note the different scales on the y-axes.

**Criteria: (1) a phenotypic change over time occurred, (2) the phenotype has an additive genetic basis, (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.*

3.2 Low spatial, temporal, and taxonomic replication

As outlined above, sufficient temporal and spatial replication is needed (1) to 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 the factors and constraints that determine a population's adaptive potential. However, only half of the 40 included studies sampled more than two timepoints (N=20) and less than half of the studies assessed genetic adaptation to climate change in at least three populations (N=15), with very few species having both spatial and temporal replication (N=7 with >2 timepoints and >2 populations, Fig. 1A, Table 1). This low temporal and spatial replication is reflected in the evidence for climate change-induced selection: few studies have strong evidence for climate change being the causal driver (N=9, Fig. 1A), by explicitly testing 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 1). The majority of the species would thus benefit from follow-up studies to infer the causal driver and the adaptive nature of the observed genetic change using increased temporal replication and strong inference methods (Merilä & Hendry, 2014). For example, increased temporal replication in field mustard (plant *Brassica rapa*) – 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, while intervening wet seasons reversed these adaptations (Hamann et al., 2018).

With sufficient temporal and spatial replication, the 40 examples we identified present exciting opportunities to test 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 (Lovell et al., 2023). For example, spatial patterns observed in key traits 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). The field could thus capitalize on the existing examples of genetic adaptation to climate change (Table 1) to test this assumption by assessing and comparing spatial and temporal signatures of climate selection.

With only 40 examples of species genetically adapting to climate change identified, taxonomic representation is very uneven. Although we found studies across nine higher taxa (Table 1), most taxa are still underrepresented, and we found no studies of genetic adaptation to climate change for fungi and amphibians. Most studies furthermore focused on the terrestrial realm (N=34), with only few examples of fresh-water species (N=4) and marine species (N=2, Table 1), and almost all studied populations are found exclusively in temperate regions in Europe and North America (Fig. S1). The scarcity of examples of genetic adaptation to climate change likely has a methodological basis, due to the lack of historical samples for most species, sampling bias, or lack of power due to insufficient temporal and/or spatial replication (Compagnoni et al., 2024; Merilä & Hendry, 2014; Urban et al., 2024). But the scarcity of examples might also mean that genetic adaptation to climate change has not occurred (yet) for many species. Our affirmative literature search – looking for populations in which genetic adaptation occurred – did not identify studies that assessed whether genetic adaptation to climate change had occurred but that did not find genetic change over time, except for two cases: some populations of plants *Arabidopsis thaliana* and *Mimulus cardinalis* showed genetic changes in flowering time in response to climate change (Table 1), whereas other populations of the same species showed no or little change [denoted as ‘but see’ in Table 1; we note that these two studies that found no or little genetic changes had some caveats, i.e. no refresher generation or missing statistical tests, see Table S2]. In addition, we are aware of more such studies that found no genetic change over time, for example in bird *Parus major* (Gienapp et al., 2006) and mammal *Marmota flaviventris* (Ozgul et al., 2010) [see for more examples (Merilä & Hendry, 2014)]. These studies often involved species with longer generation times and traits with a weak genetic basis (i.e. low heritability), which can lower the rate of adaptation. Moreover, selection can fluctuate over time, potentially hampering the likelihood of genetic adaptation (Visser et al., 2021). Our overview of taxa, species, and populations studied so far can be used to guide the design of long-term monitoring programs to improve taxonomic and ecosystem representation [e.g. (Clark et al., 2023; Jensen & Leigh, 2022; Urban et al., 2024)] to assess if genetic adaptation is indeed rare. But we also think the field could gain from strengthening the existing examples of genetic adaptation to answer this question (Table 1). In particular, we call upon the field to increase the temporal and spatial replication for these study systems, for example by resampling populations to assess the effect of fluctuations in climate change selection on genetic adaptation over time [e.g. see plant *Brassica rapa* (Hamann et al., 2018)] and comparing more populations of the same species on selection strength and standing genetic variation to investigate which factors determine the likelihood of adaptation.

3.3 Low-hanging fruit to extend ecological and taxonomic representation

Our systematic literature review identified several studies that assessed genetic adaptation to climate change in wild populations over time but that lacked strong inference (Figure 1B, N=34 papers), encompassing 81 additional species (64 plants, 9 insects, 3 birds, 2 mammals, 1 arachnid, 1 fish, 1 phytoplankton, Table S3). These studies were excluded for one of following reasons: (1) they lacked a direct comparison between two or more timepoints [N=10 papers, all range-shifting species, see below], (2) provided evidence that the trait is heritable in related species but no evidence for the focal species [N=3 papers], (3) did not provide evidence for climate change being the driver [N=12 papers], (4) did not do appropriate statistical tests [N=6 papers], and/or (5) did not account for maternal (and storage) effects, casting doubt on the observed phenotypic shift having a genetic basis [N=13 papers, see Table S2 for exclusion details]. Although not included in Table 1, with targeted follow-up studies to supplement their evidence base, these suggestive studies could similarly present 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 account for maternal (and storage) effects [N=12 papers for 69 additional species, e.g. excluding (Helm et al., 2019; Higgins et al., 2014; Nielsen et al., 2023); and excluding plant resurrection experiments without a refresher generation e.g. (Everingham et al., 2021; Gómez et al., 2018; Nevo et al., 2012); Table S2]. We 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, to be included in the list of robust examples of genetic adaptation to climate change (Table 1). 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)].

Significant opportunities exist for range shifting populations. While we assessed several papers on genetic adaption in range shifting populations (N=10 papers for 8 species: 4 insects, 2 mammals, 1 arachnid, 1 plant; Table S2 and S3), only one study presented temporal data (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 response to selection from other processes such as nonrandom dispersal and founder effects, we did not include this study here. As range shifting is being observed for many species (Lenoir & Svenning, 2015; Parmesan & Yohe, 2003), we recommend resampling range-expanded 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 a response to selection (i.e. comparing the same location and the same part of the range).

3.4 Lack of high-resolution temporal genomics studies

Only five studies of the 40 examples that show direct evidence for genetic adaptation have collected genomic data to investigate which genomic regions and underlying genes are under climate change-induced selection (N=5: three plants, one bird, one reptile, Table 1, Fig. 1A). Together, this handful of genomics studies already covers a diverse range of traits in different species as well as different climate change-induced selection pressures (Table 1). The observed patterns indicate that climate change adaptation seems to involve selection on standing genetic variation with 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 phenotypic evolution.

Despite the important insights already gleaned from these few genomics studies, spatial replication was generally low. Only two studies investigated more than one population (plant *Brassica rapa* and reptile *Anolis carolinensis*, Table 1), indicating independent adaptation trajectories for different populations and selection events (Campbell-Staton et al., 2017; Franks et al., 2016; Hamann et al., 2021). Moreover, only one of these five 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).

Our findings highlight the current lack of genomic studies using high-resolution spatial and temporal sampling of real-time climate change adaptation. Such studies would provide important information about the process and rate of evolution that studies with only two timepoints are missing. For example, a recent study using temporal genomics in Atlantic salmon (*Salmo salar*) was able to link allele frequency changes in the major effect locus *vgll3* – associated with the observed evolutionary response of younger age at maturity in male Atlantic salmon (Czorlich et al., 2018) – to fishing pressures. By analysing the *vgll3* allele frequency trajectory for 36 timepoints, Czorlich et al. (2022) could estimate the effect sizes of different fishing practices and abundance of prey species on allele frequency changes, thus showing that the fishing harvest rate of prey species determined the rate of adaptation in salmon, with a 30% decrease in allele frequency change for every unit increase of prey harvest rate. Temporal genomics studies of climate change adaptation would similarly provide highly needed opportunities to empirically test which factors drive the rate of adaptation in wild populations.

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). However, we still know little about the drivers and constraints that determine the likelihood and rate of genetic adaptation (Capblancq et al., 2020; Franks & Hoffmann, 2012). We call upon the field to capitalize on and strengthen existing examples of genetic adaptation to climate change to fill these major knowledge gaps. Here, we gathered 40 empirical examples of species from nine high-level taxa with direct evidence of genetic adaptation to climate change in wild populations. By assessing the evidence base of genetic adaptation in these studies, we identified key opportunities to investigate the conditions that allow for rapid adaptation to occur. Although for several species of animals and plants, there is evidence for a genetic shift that correlates with climate change, there are very few species with robust evidence for genetic adaptation driven by climate change (Table 1). The field could thus benefit from supplementing the evidence base of these existing samples to uncover the factors that determine a population's adaptive potential. To allow for synthesis and meta-analysis, it is especially important that raw data are made openly available, which many studies have not yet done (N=18, Table 1). Moreover, increased spatial and temporal replication are needed to find the drivers and constraints underlying the likelihood and rate of adaptation, as well as to prevent erroneous conclusions about the environmental drivers and evolutionary processes underlying the observed phenotypic changes. Especially genomic studies using high-resolution temporal sampling of real-time climate change adaptation would provide important information about the process and rate of evolution, but the field currently lacks such high-resolution temporal genomics studies. Finally, our overview of existing examples (Table 1, Fig. 1, Fig. S1) can guide the design of long-term monitoring programs to improve taxonomic and ecosystem representation. The additional 69 species we identified that had suggestive evidence of genetic adaptation to climate change are an easy place to start to extend ecological and taxonomic representation allowing for broader predictions of population responses to climate change across biodiversity, so that we can properly assess whether genetic adaptation to climate change is as rare as our results indicate.

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Author contributions

Conceptualization: N.E.v.D., B.W., M.E.V.; Methodology: N.E.v.D.; Investigation: N.E.v.D.; Data curation: N.E.v.D.; Formal analysis: N.E.v.D.; Writing - original draft: N.E.v.D.; Writing - review & editing: N.E.v.D., B.W., M.E.V.; Visualization: N.E.v.D.; Supervision: B.W., M.E.V.

Conflict of interest

The authors have 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 S1 and S2). The WoS search expression 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 et al., 2024). link for reviewer access: https://datadryad.org/stash/share/TgwQjK3o_47GnWjLcwaDn-YgtzCe8kCMwGJ7HQL4Hqc

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