Received: 30 July 2021 | Revised: 15 November 2021 | Accepted: 22 November 2021

DOI: 10.1111/mec.16299

INVITED REVIEWS AND SYNTHESES

MOLECULAR ECOLOGY WILEY

The pace of modern life, revisited

Sarah Sanderson[1] | Marc-Olivier Beausoleil[1] | Rose E. O'Dea[1,2] | Zachary T. Wood[3] | Cristian Correa[4,5] | Victor Frankel[1] | Lucas D. Gorné[1,6,7,8,9] | Grant E. Haines[1] | Michael T. Kinnison[3] | Krista B. Oke[10] | Fanie Pelletier[10] | Felipe Pérez-Jvostov[1] | Winer D. Reyes-Corral[1] | Yanny Ritchot[10] | Freedom Sorbara[1] | Kiyoko M. Gotanda[8,9] | Andrew P. Hendry[1]

[1]Department of Biology and Redpath Museum, McGill University, Montréal, Québec, Canada

[2]Evolution & Ecology Research Centre, UNSW, Sydney, New South Wales, Australia

[3]School of Biology and Ecology and Maine Center for Genetics in the Environment, University of Maine, Orono, Maine, USA

[4]Facultad de Ciencias Forestales y Recursos Naturales, Instituto de Conservación Biodiversidad y Territorio, Universidad Austral de Chile, Valdivia, Chile

[5]Centro de Humedales Río Cruces, Universidad Austral de Chile, Valdivia, Chile

[6]Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina

[7]Consejo Nacional de Investigaciones Científicas y Técnicas, CONICET, IMBiV, Córdoba, Argentina

[8]Department of Biological Sciences, Brock University, St. Catharines, Ontario, Canada

[9]Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec, Canada

[10]College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, Alaska, USA

Correspondence
Kiyoko M. Gotanda, Department of Biological Sciences, Brock University, St. Catharine's, Ontario, Canada.
Email: kgotanda@brocku.ca

Funding information
NSF, Grant/Award Number: OIA 1826777 and OAI 1849227

Abstract

Wild populations must continuously respond to environmental changes or they risk extinction. Those responses can be measured as phenotypic rates of change, which can allow us to predict contemporary adaptive responses, some of which are evolutionary. About two decades ago, a database of phenotypic rates of change in wild populations was compiled. Since then, researchers have used (and expanded) this database to examine phenotypic responses to specific types of human disturbance. Here, we update the database by adding 5675 new estimates of phenotypic change. Using this newer version of the data base, now containing 7338 estimates of phenotypic change, we revisit the conclusions of four published articles. We then synthesize the expanded database to compare rates of change across different types of human disturbance. Analyses of this expanded database suggest that: (i) a small absolute difference in rates of change exists between human disturbed and natural populations, (ii) harvesting by humans results in higher rates of change than other types of disturbance, (iii) introduced populations have increased rates of change, and (iv) body size does not increase through time. Thus, findings from earlier analyses have largely held-up in analyses of our new database that encompass a much larger breadth of species, traits, and human disturbances. Lastly, we use new analyses to explore how various types of human disturbances affect rates of phenotypic change, and we call for this database to serve as a steppingstone for further analyses to understand patterns of contemporary phenotypic change.

KEYWORDS
anthropogenic disturbance, contemporary evolution, Darwins, Haldanes, human disturbance, phenotypic traits, rapid evolution

Kiyoko M. Gotanda and Andrew P. Hendry contributed equally.

1 | INTRODUCTION

The rate at which populations can respond adaptively to environmental change will determine their ability to persist, thrive, and expand in a changing world. These adaptative responses are determined by changes in organismal phenotypes (as opposed to genotypes) – because phenotypes interface with the environment and thus are the direct determinants of fitness (Alberti et al., 2017; Endler, 1986; Hendry, 2017; Schluter, 2000). Throughout this paper, we therefore use a definition of adaptive response that includes genetic and plastic contributions to phenotypic change, and, in many cases, we cannot differentiate between the two. Historically, such adaptive phenotypic changes were thought to be very slow, as exemplified by Charles Darwin's statement that "we see nothing of these slow changes in progress until the hand of time has marked the long lapse of ages" (Darwin, 1859). This assumption began to crumble with the accumulation of studies documenting so-called "rapid evolution." Some famous early examples of this phenomenon included industrial melanism in peppered moths (Kettlewell, 1973), body size in mice colonizing islands (Berry, 1964), body size and colour in house sparrows invading North America (Johnston & Selander, 1964), and resistance of plants to pollutants found in mine tailings (Antonovics & Bradshaw, 1970). In most of these early examples from nature, it was unclear whether the observed phenotypic changes were genetic, as opposed to plastic. It was therefore game-changing when a series of common-garden experiments confirmed that at least some rapid phenotypic changes seen in nature are, in fact, genetically based (Al-Hiyaly et al., 1990; Reznick, 1982; Stearns, 1983; Wu & Kruckeberg, 1985).

At the end of the 20th century, it remained unclear if the documented cases of rapid phenotypic change were just rare exceptions or the tip of the iceberg. Resolving this uncertainty required broader literature surveys and a quantitative standard for calculating and comparing rates of phenotypic change. A precedent already existed in the literature because paleontologists had long been calculating rates of phenotypic change in fossil time series (Gingerich, 1983, 1993; Haldane, 1949). Motivated by that precedent, Hendry and Kinnison (1999) combed the literature for examples of phenotypic change on contemporary time scales and calculated rates of change using two classic metrics ("darwins" and "haldanes"). The authors concluded that "[…] *evolution as hitherto considered "rapid" may often be the norm and not the exception*" (Hendry & Kinnison, 1999). They further advocated use of the general term "contemporary evolution" because "rapid evolution" requires formal confirmation of exceptionally rapid rates. That original paper, and the follow-up analyses of Kinnison and Hendry (2001), opened the flood-gates to a series of influential papers analysing the database of rates of phenotypic change to answer a series of evolutionary questions (Alberti et al., 2017; Crispo et al., 2010; Gorné & Díaz, 2019; Gotanda et al., 2015; Hendry et al., 2008; Kinnison & Hendry, 2001; Palkovacs et al., 2011; Uyeda et al., 2011; Westley, 2011). Those studies also often made the case that evolution operates on scales fast enough to have ecological outcomes, leading the way into the field of eco-evolutionary dynamics (Des Roches et al., 2018; Fitzpatrick et al., 2015; Hendry, 2017).

BOX 1 Definitions of the different types of data included in the database

1. System: Each system has its own unique species, disturbance, and location (population). Within a given system, you can have multiple traits – for example, tarsus length and fledging date.
2. Disturbance: See Box 2.
3. Trait Classification: Traits were classified as determined by Kingsolver and Diamond (2011): size, other morphology, phenology, other life history traits, behaviour, or physiology.
4. Study type: Studies were determined to be phenotypic in nature if traits were studied in natural populations and studies were determined to be genetic in nature if they used common-garden or quantitative genetic methods (i.e., animal model analyses). We note that studies classified as phenotypic could have a genetic basis (see introduction), but that we could not determine that from the methods of the study.
5. Design: Data were determined to be either allochronic (same population/different time points) or synchronic (populations with known divergence time).
6. Data scale: Data were determined to be ratio (constant interval with a precise zero; e.g., mass or length) or interval (constant interval with an arbitrary zero; e.g., temperature or time of day).
7. Generation time: The amount of time to reproductive age, given in years.

The number of studies available for calculating rates of phenotypic change has increased dramatically over the last decade or so. Compared to the last published version of the database that contained only populations in the wild (Alberti et al., 2017), the new database published herein has increased from 1663 to 7338 rates, 89 to 214 studies, 175 to 1654 systems (Box 1), and 155 to 329 species. Hence, our first goal in the current paper is to present this new quality-controlled and much-expanded database of contemporary phenotypic changes in nature – The Phenotypic Rates of Change Evolutionary and Ecological Database (PROCEED) Version 5.0. This new database is publicly available at Dryad and https://proceeddatabase.weebly.com/. Our second goal was to use the new database to revisit and replicate previous analyses and conclusions based on earlier versions of the database. Specifically, we want to know if the effect sizes obtained in previous analyses have changed with the addition of new data. We ask four questions: (i) Does the evidence still support the conclusion from Hendry et al. (2008) that phenotypic change is greater in human-disturbed systems than in more "natural" systems (see also Alberti et al., 2017)? (ii) Does the evidence

RIGHTSLINK
1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

BOX 2 Definitions of the different types of human disturbance categories used in the updated database

- Introductions: "when humans transferred a species to a new geographical location, and comparisons were then made between introduced and ancestral populations (Carroll et al., 2005)".
- IResponse to introductions: when a local population of a species is responding to the introduction of a species.
- Landscape change: when any type of modification to the habitat of a population occurs.
- Hunting/Harvesting: when there is hunting or harvesting of a species by humans.
- Pollution: when any type of pollutant enters a system.
- Climate change: when the objectives of the study are directly linked to climate change.
- Natural: established populations that are not subject to obvious human impacts (as listed above). Generally, these studies involved the long-term monitoring of natural populations.

still support the conclusion from Darimont et al. (2009) that phenotypic changes are most rapid when humans act as predators, such as during harvesting (see also Sharpe & Hendry, 2009)? (iii) Does the evidence still support the conclusion from Westley (2011) that introduced populations do not show particularly rapid phenotypic changes, relative to non-introduced populations? (iv) Does the evidence still support the conclusion from Gotanda et al. (2015) that no evidence exists for microevolutionary trends toward increasing body size – as had been suggested in relation to "Cope's Rule" (Kingsolver & Pfennig, 2004)?

The inclusion of 5675 additional data entries might change earlier conclusions for either of two reasons: biases in earlier data compilations such as underrepresented or missing taxa and disturbances, or statistical limitations including small sample sizes associated with taxonomic levels or types of studies (i.e., genetic; Box 1). To assess the first possibility, we reanalyse the new database using the same methods as the original authors: that is, Hendry et al. (2008), Darimont et al. (2009), Westley (2011), and Gotanda et al. (2015). Through this approach, we can assess if previous approaches yield similar conclusions following the accumulation of more data. To assess the second possibility, we use updated statistical models in a comprehensive approach to ask: (v) Do any types of human disturbance stand out in terms of their effects on contemporary rates of phenotypic change (Pelletier & Coltman, 2018). We envision this last analysis as a precursor to what will surely be additional analyses of the new (and future) database with current and future statistical approaches. To synthesize, we propose a new platform for how to study and compare contemporary rates of phenotypic change in future studies.

2 | METHODS AND RESULTS

2.1 | Database development

The current database has a series of notable changes relative to earlier versions. First, we added new data that met the necessary criteria (Figure S1). First, phenotypic traits were quantified from natural populations of the same species either at two time points in the same population (allochronic) or in two populations with known divergence time from each other (synchronic). Second, they reported metadata as described in Box 1. Considering the large number of studies available, it was not possible for us to incorporate all studies where rates of changes could possibly be extracted. Instead, we added articles that came to our attention while also conducting systematic searches in Google Scholar and Web of Science. A particularly large addition was data from 1072 salmonid populations from four species (Clark et al., 2018; Oke et al., 2020). Second, we modified and expanded the categorization of types of human disturbances as defined in Box 2. Third, we proofed both old and new data entries to correct any errors. These efforts were facilitated by – whenever possible – obtaining summary data (means, sample sizes, and standard deviations) from tables or figures, or by contacting authors, from which we calculated rates of change (details below). Total numbers of rates of change for each disturbance type by study design (allochronic/synchronic), type of study (genetic/phenotypic), and taxa are presented in Table S1.

2.2 | The data

Here we outline processes common to all analyses. First, all statistical analyses were performed in R environment 4.0.5 (R Core Team, 2021). Second, we only included studies in which the number of generations elapsed was 300 or fewer (7338 rates), which is suitable for analyses of "contemporary" change (Hendry et al., 2008). Third, analyses were variously conducted using either darwins or haldanes (each in separate analyses, never combined) – because the two metrics have different biological and statistical properties, as well as different data requirements (Gingerich, 1993; Hendry & Kinnison, 1999; Hunt, 2012). Darwins are defined as the proportional change in the mean trait value in units of *e* per million years and are appropriate for data on a ratio scale, but not an interval scale (Box 1). We had 287 rates on interval scale from which we could not calculate Darwins. Darwins were calculated as

$$D = \frac{\ln\left(\bar{X}_2\right) - \ln\left(\bar{X}_1\right)}{10^6 \text{ years}},$$

where $\bar{X}_1$ and $\bar{X}_2$ are either mean trait values for one population at times 1 and 2 or mean trait values for two populations that had a common ancestor at a known time in the past, and the denominator then scales "time" per million years. Haldanes are the change in the mean

RIGHTSLINK

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

trait value in standard deviations per generation. Haldanes were calculated as

$$H = \frac{\left(\frac{\bar{X}_2}{SD_p}\right) - \left(\frac{\bar{X}_1}{SD_p}\right)}{g},$$

where $\bar{X}_1$ and $\bar{X}_2$ are the mean trait values as explained above, SD_p is the pooled standard deviation of the two samples, and g is the elapsed time in generations (i.e., number of years divided by generation length [Box 1]).

The response variable in all subsequent analyses was the numerator of the rate metric (i.e., darwin or haldane numerator). That is, to avoid self-correlation when plotting darwins and haldanes against time intervals, we use the absolute amount of change (numerators) plotted against the time interval (Hendry & Kinnison, 1999). For all analyses (except questions iii and iv), we used the mean amount of phenotypic change for a given species/system/study (Box 1) to avoid nonindependence of data points within a system (Kinnison & Hendry, 2001). Finally, we calculated effect sizes using partial η^2 to compare the original studies to the updated ones. (Note that partial η^2 represents the proportion of variation in a particular response variable that is explained by predictor variables and is therefore sensitive to the total amount a variance in a given database.) We now present analyses specific to each question, their respective results, and a brief discussion of results.

2.3 | The questions

2.3.1 | Question I: Are rates of phenotypic change greater in human-disturbed systems?

Humans cause particularly dramatic environmental changes, and so we might expect human disturbances to accelerate rates of phenotypic change. Consistent with this idea, Hendry et al. (2008) reported that phenotypic rates of change were higher for populations in human-disturbed systems than for populations in more "natural" systems that were not subject to direct human disturbance. To replicate the original analyses with our new database, we used analyses of covariance (ANCOVA) to assess whether the absolute amount of phenotypic change (darwin or haldane numerator) differed between the two general contexts (human-disturbed or natural) while controlling for the length of the time interval (years for darwins, generations for haldanes). We ran two separate analyses: one for haldane numerators and one for darwin numerators.

As in Hendry et al. (2008), our new database suggests that rates of change were generally higher in human-disturbed systems compared to natural systems (Figure 1; Figure S2). The difference between contexts (human-disturbed versus natural) was, however, much reduced in our new database (partial $\eta^2 = 0.018$) compared to the original analysis (partial $\eta^2 = 0.115$; Figure 1; Figure S2; Table 1; Table S2). This smaller difference could result from confounding effects of multiple types of disturbances (Galton, 1886; Kelly & Price, 2017; Pelletier & Coltman, 2018). That is, it can be difficult to assign a level or type of human disturbance to a particular system. For example, climate change is likely to affect all systems indirectly, including systems we have classified as "natural." Here, we classified disturbance as climate change only if the original study specifically tested for an effect of climate change. We will later return to the influence of these multiple disturbances on inferences about contemporary phenotypic change. Our expanded database could also mean that effects like winnowing, which would reduce the number of populations with low rates of phenotypic change because they are more likely to go extinct (Hendry et al., 2008), do not appear to have a strong overall effect.

By comparing estimates from wild populations to those from common-garden or animal model analyses (Box 1), Hendry et al. (2008) concluded that plasticity likely contributed substantially to the rate differences between human-disturbed and more natural contexts (Figures S3, Figure 4). That suggestion arose because the difference between contexts was lower when common-garden or animal model studies were used – and because large changes could sometimes be seen immediately after a disturbance (Hendry et al., 2008). Such patterns also occurred in the present database, supporting those original inferences (Figures S3 and S4). At the same time, it is important to note that genetic changes definitely occurred in a number of studies, but that many of the most disturbed contexts (e.g., harvesting) are not particularly amenable to the assessment of genetically-based phenotypic change. Only 24% of the phenotypic change entries in our database could be labelled as genetically based and so the contributions of plasticity versus genetic change remain unknown for the other 76%.

2.3.2 | Question II: Are particularly rapid and consistent changes associated with harvesting?

A particularly strong and consistent disturbance that directly impacts some populations occurs when humans act as a predator, such as in cases of fish harvesting. To explore this idea, Darimont et al. (2009) took the human-disturbed versus natural distinction of Hendry et al. (2008) and divided the human-disturbed systems into those experiencing direct harvesting versus those experiencing other forms of human disturbance. After adding more data, especially to the harvesting category, Darimont et al. (2009) reported that populations subject to harvesting had increased rates of phenotypic change compared to other types of human disturbance and also compared to natural systems. Here, we only used darwins (not haldanes) so as to replicate the original analysis. We replicated that analysis with our updated database using ANCOVA to compare darwin numerators associated with harvesting to those associated with other types of human disturbances (combined) and to those associated with more natural systems – while including time (years) as a covariate. We ran ANCOVAs using both mean and maximum rates of change per system to replicate the original study.

RIGHTSLINK
1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

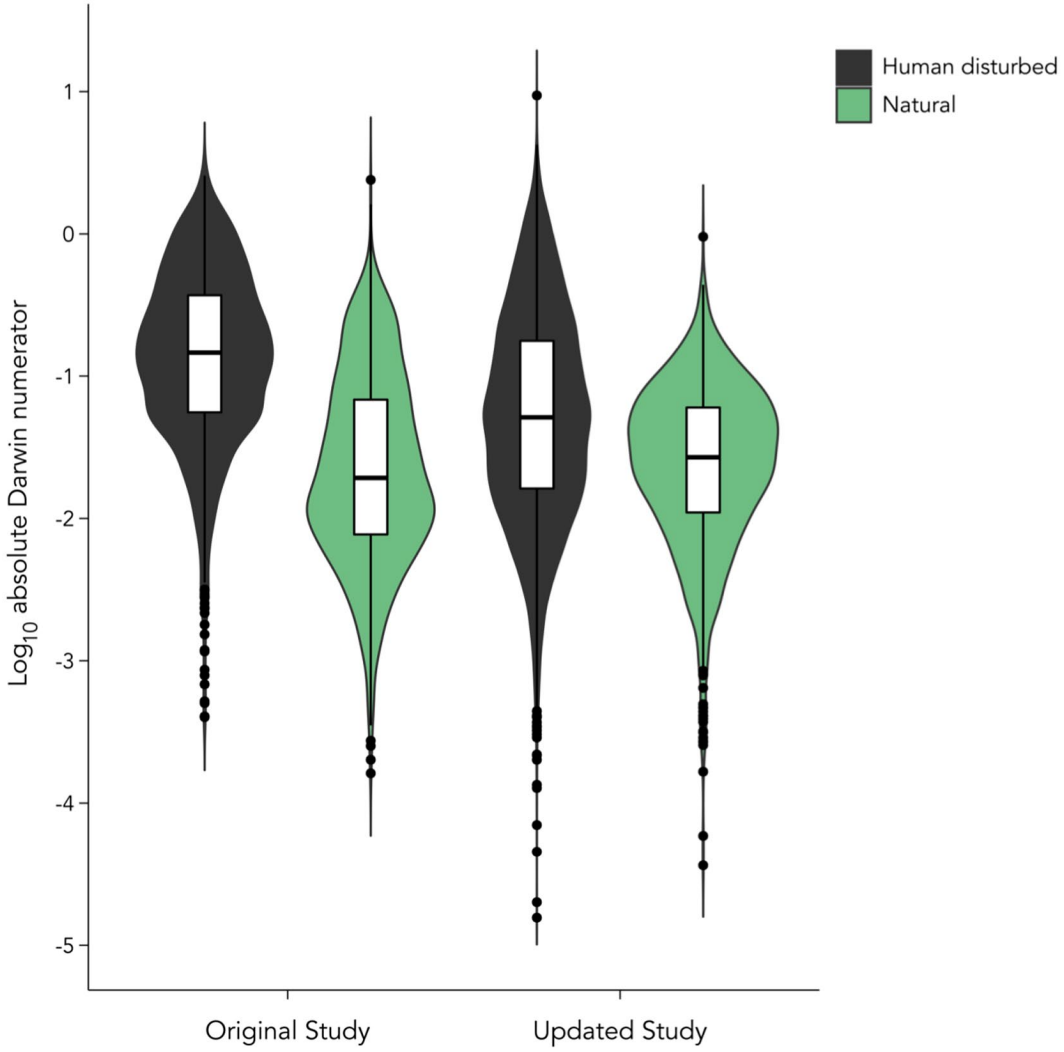

FIGURE 1 Violin plot of rates of phenotypic change (log-transformed darwin numerator) comparing natural (green) and human disturbed (black) systems. The two left violins are data from Hendry et al. (2008) and the two right violins are from our updated database. Axes were cut for better visualization (2 outliers removed from figure)

As in Darimont et al. (2009), our new analyses suggest that phenotypic changes associated with harvesting are greater than those associated with other types of human disturbances or natural systems (Figure 2; Figure S5; Table 1). However, the effect size (partial η^2) of human disturbance (three contexts: harvesting, other human disturbance, or natural) decreased substantially from 0.180 in the original study to 0.010 in the updated database (Table 1). We suggest that this decrease in effect size is mainly driven by large data sets containing many study systems with high variation. As an example, when we remove the Oke et al. (2020) and Clark et al. (2018) data sets, the effect size of human disturbance increases to 0.139 (Figure S6). Those data sets correspond to salmonid data for 1072 populations from four species over a time frame of up to 77 years. Of these populations, 60% are (or were) likely subject to harvest – and so needed to be added to that category in the present analysis. The remaining 40% of populations were added to the natural category. However, the strength and type of harvest is expected to be highly variable among those species and populations. We note that this variability in harvest strength is likely true for most harvested populations. This issue again highlights the difficulty of unambiguously assigning human disturbances to systems that are surely experiencing multiple types of disturbance that vary in intensity.

Despite the lower effect size for harvesting in our new database, we emphasize that harvested systems represented 35 of the 50 largest mean phenotypic changes in the database. Hence, it seems likely that humans as predators generate a diversity of rates of change – from many slow rates to some exceptionally high rates. Our findings continue to support the claims of fisheries and hunting wildlife scientists who have long argued for lasting phenotypic effects of harvesting on some (but not all) natural populations (Kuparinen & Festa-Bianchet, 2017; Morrissey et al., 2021; Pigeon et al., 2016; Van de Walle et al., 2018). Some of these changes are surely genetic but precise attribution to genetic versus plastic change is exceptionally difficult.

RIGHTSLINK

13655294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1 Partial η^2 values for darwin numerators and their appropriate models for each study revisited

Question	Model	N original	N updated	Explanatory variable	Effect size original	Effect size updated	*p*-original	*p*-updated
I	Absolute Darwin numerators ~ years*human influence	2844	6957	Years	0.004	0.006	.543	.562
				Human Influence	0.115	0.018	**.031**	**<.001**
II	Absolute Darwin numerators (means) ~ human influence + years	87	1529	Years	0.010	0.002	.366	.096
				Human Influence	0.180	0.010	**<.001**	**<.001**
III	Absolute Darwin numerators ~ introductions*years	104	276	Years	0.612	0.162	.954	.750
				Introductions	0.822	0.920	.480	.430
V	Log absolute Darwin numerators ~ disturbance + type + years + generations		2109	Years		0.959		
				Disturbance		0.998		
				Type		0.041		

Note: Type refers to if the data were from a phenotypic study or a genotypic study (e.g., common garden). For *p*-values for question V, see Table 4. Significant *p*-values ($p < 0.05$) are in bold.

2.3.3 | Question III: Do introduced populations show particularly rapid rates of change?

When a species is introduced to a new location, it often experiences massive shifts in biotic and abiotic conditions, which are expected to cause particularly rapid phenotypic changes (Carroll, 2007; Cox, 2004; Huey et al., 2005; Kinnison et al.,2008). However, Westley (2011) used an earlier version of this database to report that introduced populations do not – in fact – evince particularly strong or consistent phenotypic changes when compared to non-introduced populations. To replicate their analyses, we first averaged rates of change by species and then used ANCOVA to compare the magnitude of phenotypic change (darwin or haldane numerators) between introduced (disturbance classified as introduced) and non-introduced (all other disturbance categories) populations with time (years or generations) as a covariate (Westley, 2011).

We found that, on average, introduced populations show higher rates of phenotypic change than do non-introduced populations (Figure 3; Figure S7). Although the difference between introduced and non-introduced populations is marginal, the addition of new data increased the effect size (Table 1). This finding is consistent with the evidence that introduced populations do sometimes show very rapid rates of change (Figure 3). For example, zebra mussels (*Dreissena polymorpha*) introduced in European lakes rapidly shifted their growth rates (Czarnołeski et al., 2005) and Eastern grey kangaroos (*Macropus giganteus*) introduced from Tasmania to Maria Island rapidly shifted their behaviour when no longer subject to predation (Blumstein & Daniel, 2003). This type of evidence is consistent with Westley's conclusion that a small number of introduced species having very high rates of change drove the perception that introduced species generally show rapid change. Indeed, the updated database has both very high rates and very low rates of change in introduced populations (Figure 3).

In addition to large plastic responses, populations introduced to a new habitat likely experience abrupt directional selection that drives rapid evolutionary rates compared to non-introduced populations (Carroll, 2007; Cox, 2004). Once a population achieves adaptive optima and is more locally adapted, phenotypic rates of change are expected to decline with time (Figure 3). This expectation is consistent with the declining rates of change since time of introduction (figures 1 and 2 in Westley, 2011), although that pattern is also consistent with other processes (Kinnison & Hendry, 2001). These other effects include averaging rates over longer time spans or the depletion of genetic variation (Kinnison & Hairston, 2007). Finally, we note that both introduced and non-introduced populations are also experiencing other types of human disturbances that can influence their rates of change, thus potentially obscuring effects of introduction per se.

2.3.4 | Question IV: Are body sizes increasing through time?

Cope's Rule states that lineages generally evolve larger body sizes over evolutionary time (Cope, 1885). Based on an analysis of

RIGHTSLINK

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

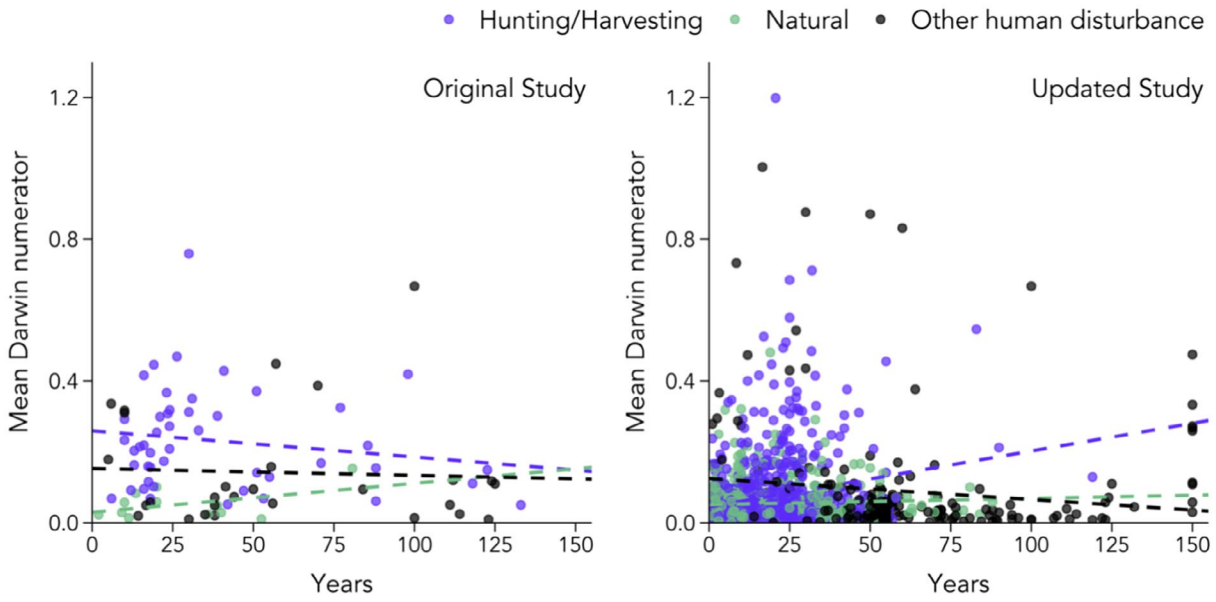

FIGURE 2 Rates of phenotypic change (mean darwin numerator) for hunted/harvested systems (purple), natural systems (green), and other types of human disturbed systems (black). Rates of change are averaged values per study system. Left panel is data from Darimont et al. (2009) and the right panel is our current database

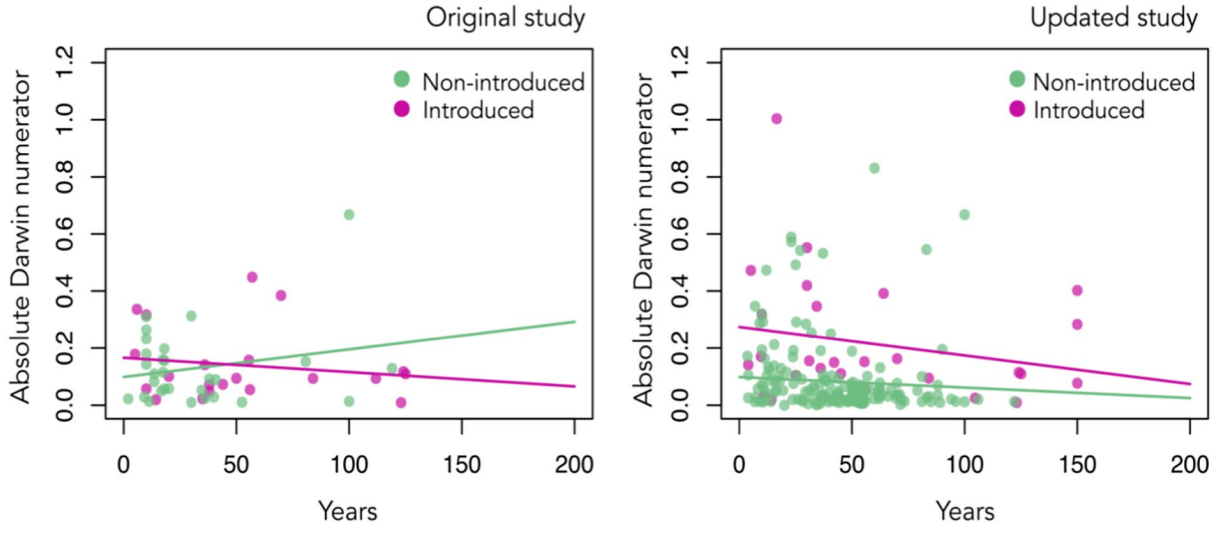

FIGURE 3 Absolute phenotypic change in introduced species (pink) and non-introduced species (green) measured in absolute darwin numerators. Each point is an expression at the species taxonomic level. Darwin numerators are plotted as a function of years. The left panel is data from Westley (2011) and the right panel is our updated database

selection estimates, Kingsolver and Pfennig (2004) argued that evidence of directional selection for larger body size in contemporary populations is consistent with a microevolutionary explanation for Cope's Rule. However, only a few studies actually support the trend suggested by Cope's Rule (Baker et al., 2015; Siepielski et al., 2019). In fact, when looking for evidence of general trends toward larger mean body size in contemporary populations, Gotanda et al. (2015) found no such trend and instead found a suggestive trend towards decreasing body size.

To replicate the analyses of Gotanda et al. (2015), we used the raw (i.e., signed, rather than absolute value) estimates of haldane or darwin numerators for allochronic studies (Box 1). The original analyses did not average rates per system or species, and so all new analyses are similarly based on individual rates. We first square-root transformed 2-D traits (e.g., surface area) and cube-root transformed 3-D traits (e.g., volume or mass) and then compared rates for body size to rates for other types of traits in a one-tailed Wilcoxon rank-sum test (see Gotanda et al., 2015 for details). We next conducted a sign test to determine whether the change in body size within populations was more commonly positive or negative. Finally, we re-ran the sign tests excluding rates calculated from populations known to be subject to harvesting – as harvesting is expected to

RIGHTSLINK

13652394x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 Pairwise Wilcoxon signed-rank test results for size versus a different phenotypic trait (one-sided) to see if rates of evolution for body size were higher than other traits

		2015				2021			
		Other morphology	Phenology	Other life history traits	Physiology	Other morphology	Phenology	Other life history traits	Physiology
Darwins	W	69,532	6326	1313	3311	999,128	89,790	192,019	50,292
	p-value	1	1	**.025**	.997	1	.938	.180	.959
Darwin numerators	W	69,428	6339	1712	3525	1,008,067	89,545	195,065	55,501
	p-value	1	1	.429	1	1	.932	.290	.999
Haldanes	W	26,355	2560	835	1316	779,302	73,446	50,376	38,219
	p-value	.821	.084	.607	.922	1	.982	.661	.924
Haldane numerators	W	26,151	3,525	773	1289	765,025	70,326	49,636	40,013
	p-value	.790	.983	.390	.889	1	.912	.585	.979

Note: Bold indicates significant *p*-values where body size rates are higher than the other phenotypic trait, though not necessarily positive. Trait classification followed the definitions found in Kingsolver and Diamond (2011).
Significant *p*-values ($p < 0.05$) are in bold.

cause particularly rapid decreases in body size (Darimont et al., 2009; Sharpe & Hendry, 2009; see question 2).

When compared to other traits, rates of change for body size are not greater (Table 2; Figure S8). As in the original analysis of Gotanda et al. (2015), rates of change in body size are more often negative (organisms are getting smaller overall), even when excluding populations subject to harvesting (Table 3; Figure 4; Figure S9). Further, rates of change for body size are not more positive (or less negative) when compared to other traits (Table 3; Figure S9), and the type of human disturbance does not appear to affect rates of change for body size (Figure 4). These results are matched by other recent analyses of body size trends in a variety of taxa (Gardner et al., 2011; Sheridan & Bickford, 2011). For instance, recent research argues that body sizes are broadly decreasing as a response to increasing temperature and variable precipitation on organismal development and growth (Fryxell et al., 2020; Sheridan & Bickford, 2011). Based on all of these findings, we emphasize that Cope's Rule is not a general rule, and rather a trend seen in certain groups of organisms (Baker et al., 2015; Rollinson & Rowe, 2015; Waller & Svensson, 2017).

2.3.5 | Question V: Does any type of disturbance stand out with respect to rates of change?

Based on the previous studies we have now revisited, as well as more recent reviews (Pelletier & Coltman, 2018), we expect associations between high rates of phenotypic change and particular types of human disturbances such as pollution (Hamilton et al., 2017), harvesting (Sullivan et al., 2017), or landscape change (Legrand et al., 2017). Using our extensive database, we are now able to ask if these or other types of human disturbances stand out with respect to rates of phenotypic change.

To answer this question, we used more advanced analyses – in contrast to the above questions that echoed previous approaches. That is, we used general linear models in which the response variables were log10-transformed absolute darwin (or haldane) numerators, and independent variables that included type of human disturbance, time (years or generations, log10-transformed), and type of study (genetic or phenotypic). Darwin and haldane numerators were analysed in separate analyses. As in question 4, we first square-root transformed 2-D traits (e.g., surface area) and cube-root transformed 3-D traits (e.g., volume or mass) before log transforming the rates. Finally, we used Tukey's post hoc tests (Hothorn et al., 2008) to explore the differential effects of disturbances on differences in rates of phenotypic change.

These new analyses suggest that time (years) had a positive effect on darwin rates of change, but type of study (genetic vs. phenotypic) did not (Table 4). The analysis using haldanes suggests similar results where time (generations) had a positive impact on haldanes, but not study type (Table S3). We also found that systems associated with pollution have the highest rates of change and that systems associated with climate change have the slowest rates of change (Figure 5; Figure S10). High rates of change due to

RIGHTSLINK

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 3 Sign-test results for rates of evolution testing whether body size rates were significantly different from zero

		2015	2021	2015 (no harvesting)	2021 (no harvesting)
Darwins	*N* (body size)	146	1902	87	705
	Median	−1763	−1306	−711	−372.842
	p-value	**<.001**	**<.001**	**.018**	**<.001**
Haldanes	N (body size)	70	1576	67	682
	Median	−0.00028	−0.0396	−0.00197	−0.0167
	p-value	.403	**<.001**	.625	**<.001**

Note: Results are shown for all data and for data with harvesting data removed. Median rates are given, and bold values mean the median is significantly different from zero. Due to the nature of the sign test, numerators yield the exact same results, and so are not reported. Body size classification followed the trait classification definitions found in Kingsolver and Diamond (2011). Significant *p* vales ($p < 0.05$) are in bold.

pollution might be explained by underlying genetic architecture where we expect evolution to occur faster when selection acts on one (or a few) loci versus polygenic traits (Kardos & Luikart, 2021; Oomen et al., 2020). In fact, many famous examples of rapid evolution are known to occur through selection on single loci such as heavy metal tolerance in plants (Macnair, 1991). In our database, most systems looking at the impact of pollution were plants, which might or might not influence the high rates for this type of disturbance. In short, more work needs to be done to explore potential interactive effects of disturbance type and taxonomic group on rates of change.

It might initially seem surprising that phenotypic changes associated with climate change were amongst the slowest. In reality, climate change has broad reaching effects and is especially difficult to assign as a particular sole causal force. Indeed, climate change must be – at some level – influencing all or most systems included in the database, regardless of the disturbance category to which we assigned them. Furthermore, studies focusing on trait change in response to climate change are likely to focus on the more gradual aspects of climate change, such as shifting seasonality and temperature increases (Parmesan & Yohe, 2003), rather than abrupt aspects such as heat waves, storms, and droughts. These more gradual aspects of climate change might also cause weak multifarious selection rather than strong selection on single genes. More importantly, climate change can be a particularly noisy environmental driver and so, is especially prone to temporal averaging (Hendry & Kinnison, 1999). In fact, few studies in nature follow populations long enough and at a fine enough temporal resolution to detect fast and large phenotypic changes (e.g., Grant & Grant, 2002). For these reasons, we also replicated the analyses by including all populations affected by climate change as "natural" (Figure S11). The results from this alternative analysis confirm that whether we have a disturbance category dedicated to climate change, or if we include climate change with "natural" systems, our conclusions do not change: climate change and natural systems are still amongst the slowest rates of evolution. Regardless, our new analysis provides the most comprehensive hypothesis (Figure 5) for how various types of disturbance differ in their effects on rates of phenotypic change.

3 | DISCUSSION

Conclusions from analyses of earlier databases of contemporary phenotypic change were largely upheld in analyses of our new database that encompasses a much larger breadth of species, traits, and human disturbances. (I) Human disturbed systems have slightly higher rates of phenotypic change then do natural systems (Figure 1). (II) Harvesting by humans results in higher rates of change compared to other types of disturbance (Figure 2). (III) Introduced populations have higher rates of change than do non-introduced populations (Figure 3). (IV) No trend is evident for increasing body size through time (Figure 4). We also use new analyses to add another tentative conclusion: (V) Systems affected by pollution have higher rates of change compared to other types of disturbances (Figure 5).

Overall, contemporary rates of phenotype change range from very slow to very fast (relative to other rates), with the latter typically gaining the most attention. This pattern is mirrored in other databases focusing on estimates of selection in natural populations (Kingsolver et al., 2001; Siepielski et al., 2013). Our database includes some striking examples of rapid phenotypic rates of change. For example, horn size in bighorn sheep (*Ovis canadensis*) decreased by 10% over 19 years when targeted by trophy hunters (Pigeon et al., 2016); zinc tolerance in tufted hairgrass (*Deschampsia cespitosa*) in zinc-contaminated soils increased by 80% over 26 years (Al-Hiyaly et al., 1990); and total egg count in soapberry bugs (*Jadera haematoloma*) adapting to an introduced host decreased by 8% over 38 years (Carroll et al., 1998). Moreover, a recent study showed rapid evolution of tusklessness in female African savanna elephants (*Loxodonta africana*) in response to poaching during the Mozambican civil war (Campbell-Staton et al., 2021). Human influences clearly shape these and many other phenotypic responses; yet high levels of variation around rates of phenotypic change make the most consistent and dramatic changes hard to confirm. In other words, phenotypic change is highly variable, likely due to various human influences but also due to the other processes that the current database cannot parse.

Our primary goal in the present paper is to make the new PROCEED database available to any researchers seeking to leverage

RIGHTSLINK

13652394x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

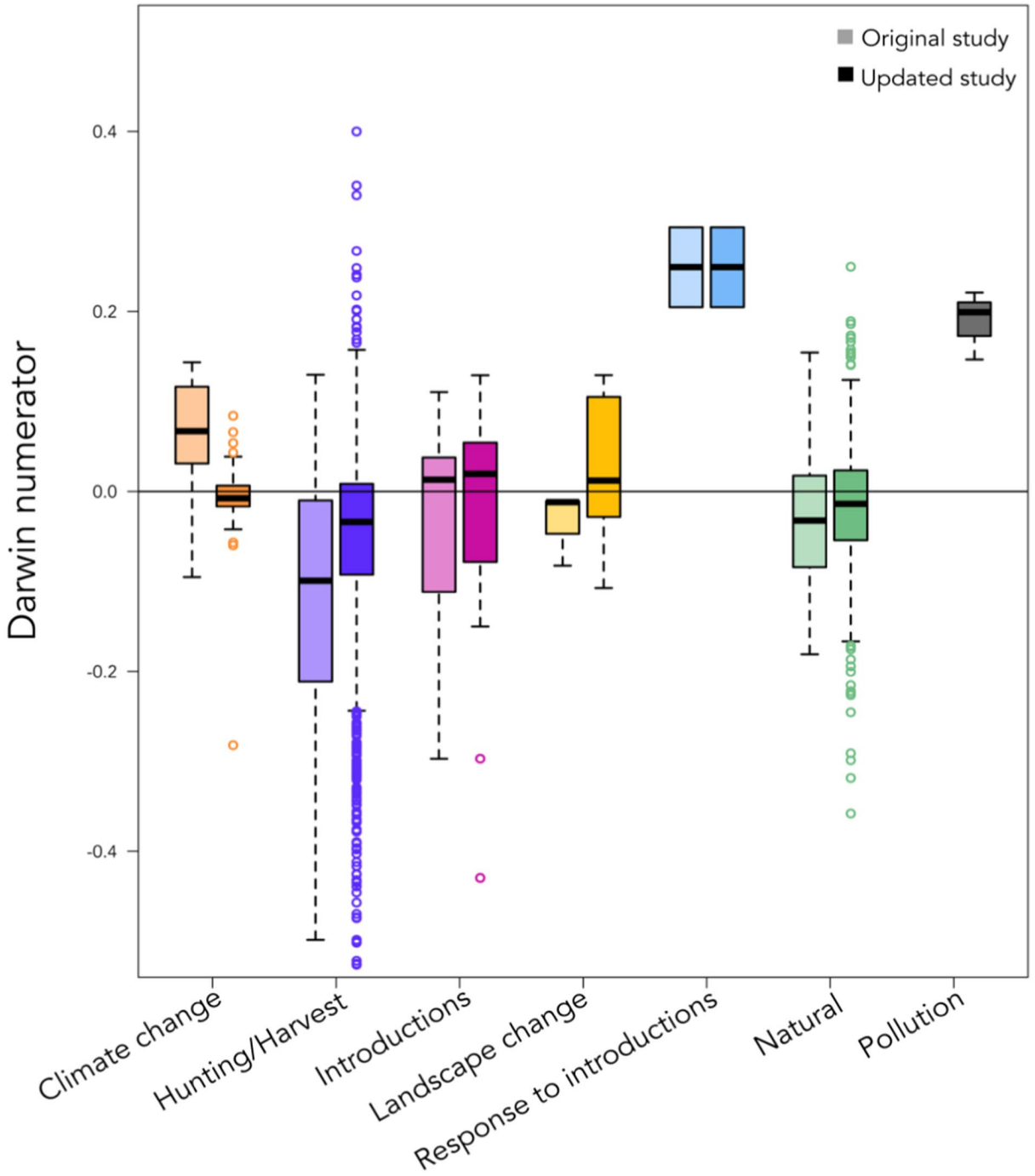

FIGURE 4 Boxplots depicting rates of change associated with body size measured in darwin numerators for each disturbance category (climate change, hunting/harvesting, introduction, landscape change, response to introductions, natural, and pollution). Light boxes are results from Gotanda et al. (2015) and dark boxes are results from our updated database. *Y*-axis was truncated to aid in visual assessment

phenotypic rates of change to answer questions in ecology, evolution, or conservation biology. For instance, we anticipate that researchers will use the new database to answer their own questions, and to better understand and predict how wild populations will respond adaptively (or not) to human disturbances. Of course, it is important to note that the current database does not formally determine whether the observed changes are adaptive or maladaptive - although the former seems more likely in most cases. We develop some examples of questions left unanswered, or only lightly broached in prior reviews, in Box 3.

Use of the PROCEED database should be accompanied with an understanding of its limits and the resulting caveats of inference.

RIGHTSLINK

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 4 Estimates, standard errors, Tukey's test categorizations, and type II likelihood ratio test results for models predicting $\log_{10}$ absolute value darwins

$\log_{10}$ darwins						
Variable	**Est.**	**SE**	**Tukey's**	χ^2	**df**	***p*-value**
Disturbance						
Climate change	−2.20	0.08	a	361.03	6	**<.001**
Hunting/harvesting	−1.54	0.07	c			
Introduction	−1.32	0.06	d			
Landscape change	−1.52	0.13	bcd			
Local response to introduced	−1.13	0.11	d			
Natural	−1.69	0.07	b			
Pollution	−0.64	0.14	e			
Phenotypic (vs. genetic)	0.01	0.06		0.06	1	.80
$\log_{10}$ years	0.15	0.02		34.76	1	**<.001**
$\log_{10}$ generations	0.05	0.04		1.48	1	.22

Note: Chi-squared values are for the variable-specific likelihood ratio tests. Significant *p*-values ($p < 0.05$) are in bold.

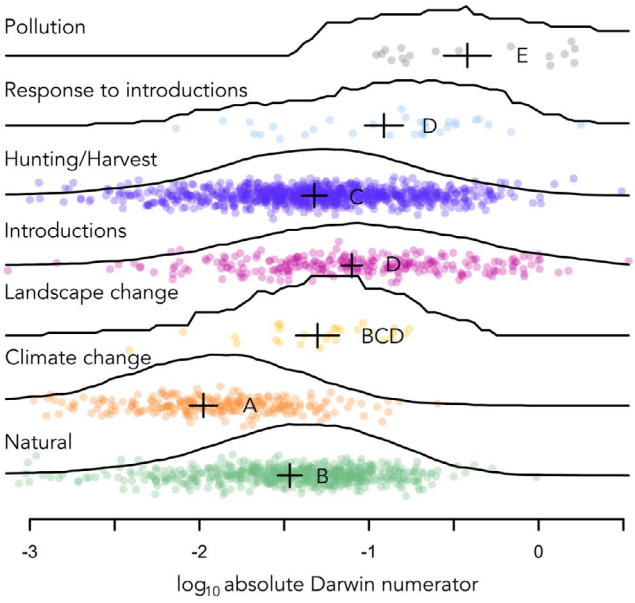

FIGURE 5 Rates of evolution—in log-transformed absolute darwin numerators—for six types of disturbances (pollution, response to introductions, hunting/harvest, introductions, landscape change, climate change) and natural populations. Points show individual data, lines show smoothed data distributions, and crosses show GLM estimates ± standard errors. Letters indicate characterisations based on Tukey's HSD tests. Each point represents a system and reference-specific average

I We suspect a strong ascertainment bias where researchers tend to focus on systems they suspect are strongly influenced by human disturbances (e.g., harvested fish populations) or where phenotypic changes are already documented (e.g., phenology). Thus, average effect sizes for a given disturbance might well decrease with the accumulation of more diverse and objective sets

BOX 3 Potential questions for future studies using the PROCEED database (https://proceeddatabase.weebly.com/)

1. Do different organisms or trait types evolve at different rates?
2. Are different disturbances generating confounding or synergistic effects?
3. What are the upper and lower limits to sustainable versus unsustainable evolutionary rates in nature?
4. Does analysing rates of change over shorter timescales (i.e., 5–10) generations, change our inferences? And, do introduced population evolve faster immediately after introductions versus many generations later?
5. Does accounting for error in statistical models change the inferences? (More studies need to publish their errors to make this possible).
6. Does considering the direction of phenotypic change (positive or negative) change the inferences from previous studies?
7. Analysing hunting/harvesting records using haldanes when more data become available.
8. Does using different types of effect sizes change the inferences?
9. Is rate of change affected by discrete versus overlapping generations?
10. To what degree do synchronic (cross population) and allochronic (time series) rates provide comparable insights into contemporary evolution over different time and space scales?

RIGHTSLINK

13652394x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

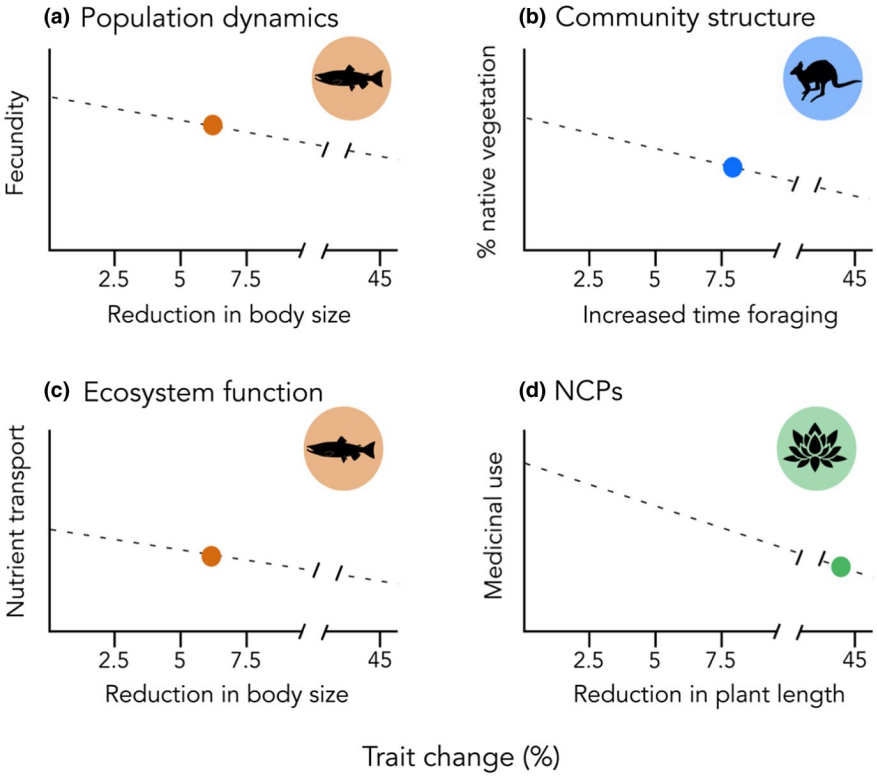

FIGURE 6 Hypothetical effects of observed phenotypic change for all levels of ecology (populations, communities, ecosystems, and nature's contribution to people [NCPs]). (a) A 5%–7% decrease in body size in harvested Chinook salmon (*Oncorhynchus tshawytscha*) in the Yukon River (Ohlberger et al., 2020) could decrease fish fecundity, affecting fishery yields. (b) An 8% increase in time spent foraging in Forester kangaroos (*Macropus giganteus*) introduced to Maria Island (Blumstein & Daniel, 2003) could affect the composition makeup of native vegetation and have effects on ecosystem processes like pollination. (c) A 5%–7% decrease in body size in harvested Chinook salmon in the Yukon River (Ohlberger et al., 2020) could decrease nutrient transport affecting ecosystem properties. (d) A 43% decrease in plant length in harvested Himalayan snow lotus (*Saussurea laniceps*; Law & Salick, 2005) will decrease plant availability for medicinal use by humans

of data – as we have shown above with the decrease in average rates of change for harvested systems after we added the 1320 rates from Oke et al. (2020) and Clark et al. (2018) (Figure S6). Those rates associated with body size declines in salmonids were calculated from data collected by the Alaska Department of Fish and Game and collaborators. As such, they represent a very broad sampling of populations across Alaska, not a narrow data set on just the most impacted populations. Another form of ascertainment bias occurs when disturbances cause some populations to go extinct, in which case their rate of phenotypic change cannot be measured (Hendry et al., 2008). It is currently unknown whether this winnowing effect of extinction (Hendry et al., 2008) biases rates upward (i.e., slower-changing populations are more likely to perish) or downward (i.e., faster-changing populations are more likely to perish – because they are experiencing more disturbance).

II Seeking to attribute a particular phenotypic change to a single disturbance (e.g., climate change) is problematic because most populations will be subject to multiple disturbances – and the degree of a given disturbance will vary dramatically among systems. Thus, we encourage future work to consider variation in disturbance intensity, rather than just disturbance presence. As examples, one can relate the strength of harvesting on populations (e.g., local catch rates) to the rate of change in size or age (e.g., Sharpe & Hendry, 2009), or the rate of climate change experienced by populations (e.g., local temperature change) to their specific rate of trait change (e.g., Franks et al., 2007; Jenni & Kéry, 2003).

III The genetic and plastic contributions to trait change remain uncertain for most traits in most systems (Merilä & Hendry, 2014). As more studies accumulate, we might be able to profitably analyse only the genetically-based phenotypic change, such as from common-garden, reciprocal transplant, or animal-model studies. Regardless, we highlight the importance of controlled experiments in combination with phenotypic change in the wild for several reasons: some populations cannot be analysed with common-garden or animal-model approaches, phenotypes measured in the laboratory might not be typical, and the "wild" is where organisms interact with their environment (Hendry, 2017).

The study of eco-evolutionary dynamics was born from the recognition of widespread contemporary evolution and the cyclical

RIGHTSLINK

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

feedback with ecological processes (Hendry, 2017). Using our database, we identified some patterns of contemporary evolution (e.g., pollution is the strongest human influence on phenotypic rates of change) and we can use this information to broaden our understanding of ecoevolutionary feedbacks in the wild. We suggest that the next step is to understand how the feedback dynamics implicit to ecoevolutionary dynamics mechanistically shape emergent patterns of contemporary evolution: are some systems more feedback prone and thus have faster or slower rates of evolution? To address such feedback dynamics, we support the development of a comprehensive database which includes not only phenotypic rates of change but also ecological and environmental rates of change and estimates of selection.

Whilst this database can be a steppingstone to further our understanding of eco-evolutionary dynamics, we also advocate that this database can allow us to move beyond "traditional" ecological and evolutionary patterns and start to consider societal consequences. In the past, the starting point for the study of contemporary evolution was often population dynamics: "perhaps the greatest contribution that evolutionary rate estimates will ultimately make is an awareness of our own role in the present microevolution of life and cautious consideration of whether populations and species can adapt rapidly enough to forestall the macroevolutionary endpoint of extinction" (Hendry & Kinnison, 1999). What is now needed is a widespread, empirical, and formal assessment of how trait changes shape ecological processes such as population dynamics, communities, and ecosystems, as well as the societal consequences such as the health and well-being of people (e.g., the impact of nature's contribution to people (NCPs) (Des Roches et al., 2018; Hendry, 2017; Hendry et al., 2017; Palkovacs et al., 2012; Stange et al., 2021; Figure 6). Oke et al., (2020) provide a compelling example, by comparing the average body size of Alaskan chinook salmon pre-1990 to the average post-2010. The authors estimate that the overall average 8% decrease in salmon body length could – all else being equal – translate into a 16% decrease in number of eggs per female, a 28% decrease in transport of marine-derived phosphorous into freshwater, a 26% reduction in average number of meals provided per fish for people in subsistence communities, and a 21% decrease in price per pound for commercial fishers.

We would like to close by re-emphasizing that the most dramatic progress will be made through studies that explicitly examine the consequences of phenotypic change. That is, more studies should formally calculate the importance of observed (and predicted) phenotypic change for all levels of ecology (populations, communities, ecosystems) and for people (nature's contributions to people). Determining the genetic and plastic contributions to that change (and its consequences) can then help to determine the limits and opportunities for enhancing or arresting trait changes via conservation and management actions. We here present a hypothetical scenario of such a study using observed rates of change (Figure 6) where the amount of phenotypic change is correlated with an ecological process that is linked to nature's contributions to people. The present study is not the end of an inspiring era of contemporary evolution – it is instead, just the start of future research on not only contemporary evolution, but also on contemporary ecoevolutionary dynamics.

ACKNOWLEDGEMENTS

This work has been supported by NSF OIA 1826777 and NSF OAI 1849227 received by Michael Kinnison, and by an NSERC Discovery Grant and Canada Research Chair to Andrew Hendry. We thank the numerous researchers that shared their data and contributed to the development of The Phenotypic Rates of Change Evolutionary and Ecological Database (PROCEED) Version 5.0. We are especially grateful to both the Carnegie Museum of Natural History and the Powdermill Avian Research Centre for sharing their data.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Ideas: Sarah Sanderson, Marc-Olivier Beausoleil, Rose E. O'Dea, Victor Frankel, Michael T. Kinnison, Andrew P. Hendry, Kiyoko M. Gotanda, and Cristian Correa. Data contributions: Sarah Sanderson, Marc-Olivier Beausoleil, Grant E. Haines, Rose E. O'Dea, Winer Daniel Reyes-Corral, Krista B. Oke, Kiyoko M. Gotanda, Yanny Ritchot, Lucas D. Gorné, Felipe Pérez-Jvostov, Zachary T. Wood, Andrew P. Hendry. Analyses: Sarah Sanderson, Marc-Olivier Beausoleil, Cristian Correa, Rose E. O'Dea, Zachary T. Wood, and Kiyoko M. Gotanda. Writing: Sarah Ssanderson, Kiyoko M. Gotanda, and Andrew P. Hendry, with contributions from all authors.

DATA AVAILABILITY STATEMENT

The data set used in this manuscript will be archived on Dryad (https://doi.org/10.5061/dryad.dz08kprxx) and is available at https://proceeddatabase.weebly.com/.

[dataset] Sarah Sanderson, Marc-Olivier Beausoleil, Rose E. O'Dea, Zachary T. Wood, Cristian Correa, Victor Frankel, Lucas D. Gorné, Grant E. Haines, Michael T. Kinnison, Krista B. Oke, Fanie Pelletier, Felipe Pérez-Jvostov, Winer Daniel Reyes-Corral, Yanny Ritchot, Freedom Sorbara, Kiyoko M. Gotanda, and Andrew P. Hendry; 2021; Database reference: Phenotypic Rates of Change Evolutionary and Ecological Database (PROCEED). https://proceeddatabase.weebly.com; Version 5.0 and Dryad: https://doi.org/10.5061/dryad.dz08kprxx.

ORCID

Sarah Sanderson https://orcid.org/0000-0003-1525-2326
Marc-Olivier Beausoleil https://orcid.org/0000-0003-3717-3223
Rose E. O'Dea https://orcid.org/0000-0001-8177-5075
Zachary T. Wood https://orcid.org/0000-0001-7369-9199
Cristian Correa https://orcid.org/0000-0002-8608-6858
Lucas D. Gorné https://orcid.org/0000-0003-1940-1755

RIGHTSLINK

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Grant E. Haines https://orcid.org/0000-0001-9085-0022
Michael T. Kinnison https://orcid.org/0000-0003-4211-2118
Krista B. Oke https://orcid.org/0000-0002-5415-3534
Fanie Pelletier https://orcid.org/0000-0002-0113-5412
Felipe Pérez-Jvostov https://orcid.org/0000-0003-0822-5039
Kiyoko M. Gotanda https://orcid.org/0000-0002-3666-0700
Andrew P. Hendry https://orcid.org/0000-0002-4807-6667

REFERENCES

Alberti, M., Correa, C., Marzluff, J. M., Hendry, A. P., Palkovacs, E. P., Gotanda, K. M., Hunt, V. M., Apgar, T. M., & Zhou, Y. (2017). Global urban signatures of phenotypic change in animal and plant populations. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(34), 8951–8956. https://doi.org/10.1073/pnas.1606034114

Al-Hiyaly, S. A. K., Mcneilly, T., & Bradshaw, A. D. (1990). The effect of zinc contamination from electricity pylons. Contrasting patterns of evolution in five grass species. *New Phytologist*, *114*(2), 183–190. https://doi.org/10.1111/j.1469-8137.1990.tb00389.x

Antonovics, J., & Bradshaw, A. D. (1970). Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity*, *25*, 349–362. https://doi.org/10.1038/hdy.1970.36

Baker, J., Meade, A., Pagel, M., & Venditti, C. (2015). Adaptive evolution toward larger size in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(16), 5093–5098. https://doi.org/10.1073/pnas.1419823112

Berry, R. J. (1964). The evolution of an island population of the house mouse. *Evolution*, *18*(3), 468–483. https://doi.org/10.2307/2406357

Blumstein, D. T., & Daniel, J. C. (2003). Foraging behavior of three Tasmanian macropodid marsupials in response to present and historical predation threat. *Ecography*, *26*(5), 585–594. https://doi.org/10.1034/j.1600-0587.2003.03516.x

Campbell-Staton, S. C., Arnold, B. J., Gonçalves, D., Granli, P., Poole, J., Long, R. A., & Pringle, R. M. (2021). Ivory poaching and the rapid evolution of tusklessness in African elephants. *Science*, *374*(6566), 483–487. https://doi.org/10.1126/science.abe7389

Carroll, S. P. (2007). Natives adapting to invasive species: Ecology, genes, and the sustainability of conservation. *Ecological Research*, *22*(6), 892–901. https://doi.org/10.1007/s11284-007-0352-5

Carroll, S. P., Klassen, S. P., & Dingle, H. (1998). Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. *Evolutionary Ecology*, *12*(8), 955–968. https://doi.org/10.1023/A:1006568206413

Carroll, S. P., Loye, J. E., Dingle, H., Mathieson, M., Famula, T. R., & Zalucki, M. P. (2005). And the beak shall inherit—Evolution in response to invasion. *Ecology Letters*, *8*(9), 944–951. https://doi.org/10.1111/j.1461-0248.2005.00800.x

Clark, J., Brenner, R., & Lewis, B. (2018). *Compiled age, sex, and length data for Alaskan salmon, 1922-2017*. https://doi.org/10.5063/F1707ZTM

Cope, E. D. (1885). On the evolution of the vertebrata, progressive and retrogressive (continued). *The American Naturalist*, *19*, 341–353. https://doi.org/10.1086/273923

Cox, G. W. (2004). *Alien species and evolution: The evolutionary ecology of exotic plants, animals, microbes, and interacting native species*. Island Press.

Crispo, E., Dibattista, J. D., Correa, C., Thibert-plante, X., Mckellar, A. E., Schwartz, A. K., & Hendry, A. P. (2010). The evolution of phenotypic plasticity in response to anthropogenic disturbance. *Evolutionary Ecology Research*, *12*, 47–66. https://doi.org/10.1088/0004-637X/742/2/126

Czarnołeski, M., Kozlowski, J., Lewandowski, K., Mikolajczyk, M., Müller, T., & Stanczykowska, A. (2005). Optimal resource allocation explains changes in the zebra mussel growth pattern through time. *Evolutionary Ecology Research*, *7*, 821–835.

Darimont, C. T., Carlson, S. M., Kinnison, M. T., Paquet, P. C., Reimchen, T. E., & Wilmers, C. C. (2009). Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(3), 952–954. https://doi.org/10.1073/pnas.0809235106

Darwin, C. (1859). *On the Origin of Species by means of natural selection, or preservation of flavoured races in the struggle for life*. John Murray.

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, *2*(1), 57–64. https://doi.org/10.1038/s41559-017-0402-5

Endler, J. A. (1986). *Natural selection in the wild* (p. 336). Princeton University Press.

Fitzpatrick, C. R., Agrawal, A. A., Basiliko, N., Hastings, A. P., Isaac, M. E., Preston, M., & Johnson, M. T. J. (2015). The importance of plant genotype and contemporary evolution for terrestrial ecosystem processes. *Ecology*, *96*(10), 2632–2642. https://doi.org/10.1890/14-2333.1

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

Fryxell, D. C., Hoover, A. N., Alvarez, D. A., Arnesen, F. J., Benavente, J. N., Moffett, E. R., Kinnison, M. T., Simon, K. S., & Palkovacs, E. P. (2020). Recent warming reduces the reproductive advantage of large size and contributes to evolutionary downsizing in nature. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1928), 20200608. https://doi.org/10.1098/rspb.2020.0608

Galton, F. (1886). Regression towards mediocrity in hereditary stature. *The Journal of the Anthropological Institute of Great Britain and Ireland*, *15*, 246–263. https://doi.org/10.2307/2841583

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, *26*(6), 285–291. https://doi.org/10.1016/j.tree.2011.03.005

Gingerich, P. (1983). Rates of evolution: Effects of time and temporal scaling. *Science*, *222*, 159–162. https://doi.org/10.1126/science.222.4620.159

Gingerich, P. (1993). Quantification and comparison of evolutionary rates. *American Journal of Science*, *293-A*, 453–478. https://doi.org/10.2475/ajs.293.A.453

Gorné, L. D., & Díaz, S. (2019). Meta-analysis shows that rapid phenotypic change in angiosperms in response to environmental change is followed by stasis. *The American Naturalist*, *194*(6), 840–853. https://doi.org/10.1086/705680

Gotanda, K. M., Correa, C., Turcotte, M. M., Rolshausen, G., & Hendry, A. P. (2015). Linking macrotrends and microrates: Re-evaluating microevolutionary support for Cope's rule. *Evolution*, *69*(5), 1345–1354. https://doi.org/10.1111/evo.12653

Grant, P. R., & Grant, B. R. (2002). Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, *296*(5568), 707–711. https://doi.org/10.1126/science.1070315

Haldane, J. B. S. (1949). Suggestions as to quantitative measurement of rates of evolution. *Evolution*, *3*(1), 51–56. https://doi.org/10.2307/2405451

Hamilton, P. B., Rolshausen, G., Uren Webster, T. M., & Tyler, C. R. (2017). Adaptive capabilities and fitness consequences associated with pollution exposure in fish. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *372*(1712), 20160042. https://doi.org/10.1098/rstb.2016.0042

Hendry, A. P. (2017). *Eco-evolutionary dynamics*. Princeton University Press.

RIGHTSLINK

13652394x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, *17*(1), 20–29. https://doi.org/10.1111/j.1365-294X.2007.03428.x

Hendry, A. P., Gotanda, K. M., & Svensson, E. I. (2017). Human influences on evolution, and the ecological and societal consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712). https://doi.org/10.1098/rstb.2016.0028

Hendry, A. P., & Kinnison, M. T. (1999). Perspective: The pace of modern life: Measuring rates of contemporary microevolution. *Evolution*, *53*(6), 1637–1653. https://doi.org/10.2307/2640428

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Huey, R., Gilchrist, G., & Hendry, A. P. (2005). Using invasive species to study evolution: Case studies with *Drosophila* and salmon. In Sax, D. F., Stachowicz, J. J. & Gaines, S. D., (eds), *Species invasions: Insights into ecology, evolution and biogeography*, (p. 139+164). Sinauer Associates.

Hunt, G. (2012). Measuring rates of phenotypic evolution and the inseparability of tempo and mode. *Paleobiology*, *38*(03), 351–373. https://doi.org/10.1666/11047.1

Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1523), 1467–1471. https://doi.org/10.1098/rspb.2003.2394

Johnston, R. F., & Selander, R. K. (1964). House sparrows: Rapid evolution of races in North America. *Science*, *144*(3618), 548–550. https://doi.org/10.1126/science.144.3618.548

Kardos, M., & Luikart, G. (2021). The genetic architecture of fitness drives population viability during rapid environmental change. *The American Naturalist*, *197*(5), 511–525. https://doi.org/10.1086/713469

Kelly, C., & Price, P. D. (2017). Correcting for regression to the mean in behavior and ecology. *The American Naturalist*, *166*(6), 700. https://doi.org/10.2307/3491232

Kettlewell, H. (1973). *Evolution of melanism: The study of a recurring necessity*. Clarendon Press.

Kingsolver, J. G., & Diamond, S. E. (2011). Phenotypic selection in natural populations: What limits directional selection? *The American Naturalist*, *177*(3), 346–357. https://doi.org/10.1086/658341

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P., & Beerli, P. (2001). The strength of phenotypic selection in natural populations. *The American Naturalist*, *157*(3), 245–261. https://doi.org/10.1086/319193

Kingsolver, J., & Pfennig, D. (2004). Individual-level selection as a cause of Cope's Rule of phyletic size increase. *Evolution*, *58*, 1608–1612. https://doi.org/10.1111/j.0014-3820.2004.tb01740.x

Kinnison, M. T., & Hairston, N. G. (2007). Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. *Functional Ecology*, *21*(3), 444–454. https://doi.org/10.1111/j.1365-2435.2007.01278.x

Kinnison, M. T., & Hendry, A. P. (2001). The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica*, *112*(1), 145–8. https://doi.org/10.1023/A:1013368628607

Kinnison, M. T., Unwin, M. J., & Quinn, T. P. (2008). Eco-evolutionary vs. Habitat contributions to invasion in salmon: Experimental evaluation in the wild. *Molecular Ecology*, *17*(1), 405–414. https://doi.org/10.1111/j.1365-294X.2007.03495.x

Kuparinen, A., & Festa-Bianchet, M. (2017). Harvest-induced evolution: Insights from aquatic and terrestrial systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160036. https://doi.org/10.1098/rstb.2016.0036

Law, W., & Salick, J. (2005). Human-induced dwarfing of Himalayan snow lotus, *Saussurea laniceps* (Asteraceae). *Proceedings of the National Academy of Sciences of the United States of America*, *102*(29), 10218–10220. https://doi.org/10.1073/pnas.0502931102

Legrand, D., Cote, J., Fronhofer, E. A., Holt, R. D., Ronce, O., Schtickzelle, N., Travis, J. M. J., & Clobert, J. (2017). Eco-evolutionary dynamics in fragmented landscapes. *Ecography*, *40*(1), 9–25. https://doi.org/10.1111/ecog.02537

Macnair, M. R. (1991). Why the evolution of resistance to anthropogenic toxins normally involves major gene changes: The limits to natural selection. *Genetica*, *84*(3), 213–219. https://doi.org/10.1007/BF00127250

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

Morrissey, M. B., Hubbs, A., & Festa-Bianchet, M. (2021). Horn growth appears to decline under intense trophy hunting, but biases in hunt data challenge the interpretation of the evolutionary basis of trends. *Evolutionary Applications*, *14*(6), 1519–1527. https://doi.org/10.1111/eva.13207

Ohlberger, J., Schindler, D. E., Brown, R. J., Harding, J. M. S., Adkison, M. D., Munro, A. R., Horstmann, L., & Spaeder, J. (2020). The reproductive value of large females: Consequences of shifts in demographic structure for population reproductive potential in Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(8), 1292–1301. https://doi.org/10.1139/cjfas-2020-0012

Oke, K. B., Cunningham, C. J., Westley, P. A. H., Baskett, M. L., Carlson, S. M., Clark, J., Hendry, A. P., Karatayev, V. A., Kendall, N. W., Kibele, J., Kindsvater, H. K., Kobayashi, K. M., Lewis, B., Munch, S., Reynolds, J. D., Vick, G. K., & Palkovacs, E. P. (2020). Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications*, *11*(1), 4155. https://doi.org/10.1038/s41467-020-17726-z

Oomen, R. A., Kuparinen, A., & Hutchings, J. A. (2020). Consequences of single-locus and tightly linked genomic architectures for evolutionary responses to environmental change. *Journal of Heredity*, *111*(4), 319–332. https://doi.org/10.1093/jhered/esaa020

Palkovacs, E. P., Kinnison, M. T., Correa, C., Dalton, C. M., & Hendry, A. P. (2012). Fates beyond traits: Ecological consequences of human-induced trait change. *Evolutionary Applications*, *5*(2), 183–191. https://doi.org/10.1111/j.1752-4571.2011.00212.x

Palkovacs, E. P., Wasserman, B. A., & Kinnison, M. T. (2011). Eco-evolutionary trophic dynamics: Loss of top predators drives trophic evolution and ecology of prey. *PLoS One*, *6*(4), e18879. https://doi.org/10.1371/journal.pone.0018879

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pelletier, F., & Coltman, D. W. (2018). Will human influences on evolutionary dynamics in the wild pervade the Anthropocene? *BMC Biology*, *16*(1), 1–10. https://doi.org/10.1186/s12915-017-0476-1

Pigeon, G., Festa-Bianchet, M., Coltman, D. W., & Pelletier, F. (2016). Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications*, *9*(4), 521–530. https://doi.org/10.1111/eva.12358

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reznick, D. (1982). The impact of predation on life history evolution in Trinidadian Guppies: Genetic basis of observed life history patterns. *Evolution*, *36*(6), 1236–1250. https://doi.org/10.2307/2408156

Rollinson, N., & Rowe, L. (2015). Persistent directional selection on body size and a resolution to the paradox of stasis. *Evolution*, *69*(9), 2441–2451. https://doi.org/10.1111/evo.12753

Schluter, D. (2000). Ecological character displacement in adaptive radiation. *The American Naturalist*, *156*(4), S4–S16. https://doi.org/10.2307/3079223

RIGHTSLINK

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Sharpe, D. M. T., & Hendry, A. P. (2009). Life history change in commercially exploited fish stocks: An analysis of trends across studies. *Evolutionary Applications*, *2*(3), 260–275. https://doi.org/10.1111/j.1752-4571.2009.00080.x

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Siepielski, A. M., Gotanda, K. M., Morrissey, M. B., Diamond, S. E., DiBattista, J., & Carlson, S. M. (2013). The spatial patterns of directional phenotypic selection. *Ecology Letters*, *16*(11), 1382–1392. https://doi.org/10.1111/ele.12174

Siepielski, A. M., Morrissey, M. B., Carlson, S. M., Francis, C. D., Kingsolver, J. G., Whitney, K. D., & Kruuk, L. E. B. (2019). No evidence that warmer temperatures are associated with selection for smaller body sizes. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1907), 20191332. https://doi.org/10.1098/rspb.2019.1332

Stange, M., Barrett, R. D. H., & Hendry, A. P. (2021). The importance of genomic variation for biodiversity, ecosystems and people. *Nature Reviews Genetics*, *22*(2), 89–105. https://doi.org/10.1038/s41576-020-00288-7

Stearns, S. C. (1983). The genetic basis of differences in life-history traits among six populations of Mosquitofish (*Gambusia affinis*) that shared ancestors in 1905. *Evolution*, *37*(3), 618–627. https://doi.org/10.2307/2408274

Sullivan, A. P., Bird, D. W., & Perry, G. H. (2017). Human behaviour as a long-term ecological driver of non-human evolution. *Nature Ecology & Evolution*, *1*(3), 1–11. https://doi.org/10.1038/s41559-016-0065

Uyeda, J. C., Hansen, T. F., Arnold, S. J., & Pienaar, J. (2011). The million-year wait for macroevolutionary bursts. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(38), 15908–15913. https://doi.org/10.1073/pnas.1014503108

Van de Walle, J., Pigeon, G., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2018). Hunting regulation favors slow life histories in a large carnivore. *Nature Communications*, *9*(1), 1100. https://doi.org/10.1038/s41467-018-03506-3

Waller, J. T., & Svensson, E. I. (2017). Body size evolution in an old insect order: No evidence for Cope's Rule in spite of fitness benefits of large size. *Evolution*, *71*(9), 2178–2193. https://doi.org/10.1111/evo.13302

Westley, P. A. H. (2011). What invasive species reveal about the rate and form of contemporary phenotypic change in nature. *The American Naturalist*, *177*(4), 496–509. https://doi.org/10.1086/658902

Wu, L., & Kruckeberg, A. L. (1985). Copper tolerance in two legume species from a copper mine habitat. *New Phytologist*, *99*(4), 565–570. https://doi.org/10.1111/j.1469-8137.1985.tb03684.x

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Sanderson, S., Beausoleil, M.-O., O'Dea, R. E., Wood, Z. T., Correa, C., Frankel, V., Gorné, L. D., Haines, G. E., Kinnison, M. T., Oke, K. B., Pelletier, F., Pérez-Jvostov, F., Reyes-Corral, W. D., Ritchot, Y., Sorbara, F., Gotanda, K. M., & Hendry, A. P. (2022). The pace of modern life, revisited. *Molecular Ecology*, 31, 1028–1043. https://doi.org/10.1111/mec.16299

1365294x, 2022, 4, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.16299 by Cambridge University Library, Wiley Online Library on [28/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

RIGHTSLINK