Received: 8 November 2022 | Revised: 30 January 2023 | Accepted: 1 February 2023

DOI: 10.1111/ele.14186

LETTER

ECOLOGY LETTERS cnrs WILEY

Contemporary changes in phenotypic variation, and the potential consequences for eco-evolutionary dynamics

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Funding information
Faculty of Mathematics and Science at Brock University; Marine Agricultural and Forest Experiment Station; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: 569441-2022; Office of Integrative Activities, Grant/Award Number: 1849227 and 2222339

Editor: Stephan Munch

Abstract

Most studies assessing rates of phenotypic change focus on population mean trait values, whereas a largely overlooked additional component is changes in population trait variation. Theoretically, eco-evolutionary dynamics mediated by such changes in trait variation could be as important as those mediated by changes in trait means. To date, however, no study has comprehensively summarised how phenotypic variation is changing in contemporary populations. Here, we explore four questions using a large database: How do changes in trait variances compare to changes in trait means? Do different human disturbances have different effects on trait variance? Do different trait types have different effects on changes in trait variance? Do studies that established a genetic basis for trait change show different patterns from those that did not? We find that changes in variation are typically small; yet we also see some very large changes associated with particular disturbances or trait types. We close by interpreting and discussing the implications of our findings in the context of eco-evolutionary studies.

KEYWORDS

coefficient of variation, eco-evolutionary dynamics, human disturbances, natural populations, phenotypic change, variation

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INTRODUCTION

Hundreds of studies have shown that ecology shapes evolution (eco-to-evo) by altering phenotypes through phenotypic plasticity or genotypic change, and that these changes are amplified by human disturbances (Alberti et al., 2017; Gorné & Díaz, 2019; Hendry & Kinnison, 1999; Reznick & Ghalambor, 2001). Such phenotypic changes, including those confirmed to be 'evolutionary', can occur over time-scales short enough for humans to observe in the present time; that is, they are 'contemporary' (Darimont et al., 2009; Hendry & Kinnison, 1999; Sanderson et al., 2021). Some classical examples include industrial melanism in peppered moths (Kettlewell, 1973), resistance to pollutants in plants along mine tailings (Antonovics & Bradshaw, 1970) and changes in beak size in Darwin's finches (Grant & Grant, 2006). More recently, attention also has been drawn to the reciprocal (evo-to-eco) pathway: that is, contemporary phenotypic changes can shape ecology through altered interactions between organisms and their environment (Brunner et al., 2019; Hendry, 2017). As just one example, mesocosm experiments have shown that different life history phenotypes of Trinidadian guppies (i.e. high predation guppies typically grow faster, mature earlier and produce more offspring than do low predation guppies) have important effects on ecosystem functions such as nutrient cycling, nutrient fluxes, ecosystem function, metabolism and leaf litter decomposition (review: El-Sabaawi et al., 2015). Both pathways are expected to be particularly important when human (as opposed to more 'natural') disturbances dramatically alter environments (Hendry et al., 2017).

All about the mean

The vast majority of eco-evolutionary studies, whether focusing on the eco-to-evo or evo-to-eco pathways, have considered changes in population mean trait values (Alberti et al., 2017; Gorné & Díaz, 2019; Hendry et al., 2008; Sanderson et al., 2021). That is, work on the eco-to-evo pathway emphasises how ecology drives changes in the mean trait values of populations, and work on the evo-to-eco pathway emphasises how changes in phenotypic mean trait values influence populations, communities and ecosystems. These effects can arise in two major ways (Hendry, 2017). First, changes in mean phenotypes can alter population dynamics (Cameron et al., 2014; Dibble & Rudolf, 2019; Thompson et al., 2022), such that better-adapted populations can have higher mean fitness, faster population growth, larger population size, or greater resilience. These adaptation-driven changes in population dynamics then can alter community structure and ecosystem function. Second, changes in mean phenotypes can alter per-capita effects on communities and ecosystems, such as when changes in predator foraging traits alter their prey population and, hence, their prey community (Moya-Laraño et al., 2014; Palkovacs & Post, 2008, 2009). These two major pathways are not mutually exclusive given that per-capita effects can also depend on overall density.

Although earlier discussions of these processes did not focus on human effects in particular, it has become clear that changes in the mean phenotypes of organisms accelerate under certain types of human disturbance (Alberti et al., 2017; Darimont et al., 2009; Sanderson et al., 2021), and that those phenotypic changes influence ecosystem services and nature's contribution to people. In one concrete example, Oke et al. (2020) documented an 8% decrease in the mean body size of Alaskan Chinook salmon pre-1990 to post-2010 and estimated corresponding losses for ecosystem services and nature's contribution to people: 16% decrease in egg production, 28% decrease in nutrient transport, a 26% reduction in meals for rural people and a 21% decrease in fisheries value (Clark et al., 2018; Oke et al., 2020). Similar eco-evolutionary effects will surely accompany changes in other organisms that are harvested by people or that influence the ecosystems on which humans depend.

What about the variation?

Extending beyond this previous work on changes in trait means, we here focus attention on another component of eco-evolutionary dynamics: contemporary changes in trait variation—such as might be indexed by within-population phenotypic variance (Bolnick et al., 2003; Maciejewski et al., 2020). We argue that focusing only on changes in trait means can misrepresent the functional consequences of trait variation for two reasons. First, changes in trait variation could be—at least in principle—as *important* for populations, communities, ecosystems and nature's contribution to people as are changes in trait means. Second, the causes and consequences of changes in trait variation could be fundamentally *different* from the causes and consequences of changes in trait means. For example, individuals in the tails of phenotypic distributions can have disproportionate ecological effects such that they are 'keystone individuals' (Modlmeier et al., 2014). For example, Sih and Watters (2005) found that the presence of hyperaggressive individual male water striders strongly changed mating dynamics at the population level.

Ecology is expected to change trait variation (eco-to-evo) through processes that increase, decrease or maintain genetic variation, as well as processes that modify the expression of phenotypes for a given genotype (Figure 1). For instance, within-population variation is expected to increase through mutations, recombination, gene flow and developmental noise; whereas variation is expected to decrease due to genetic drift (e.g. inbreeding, founder effects) and certain types of biased

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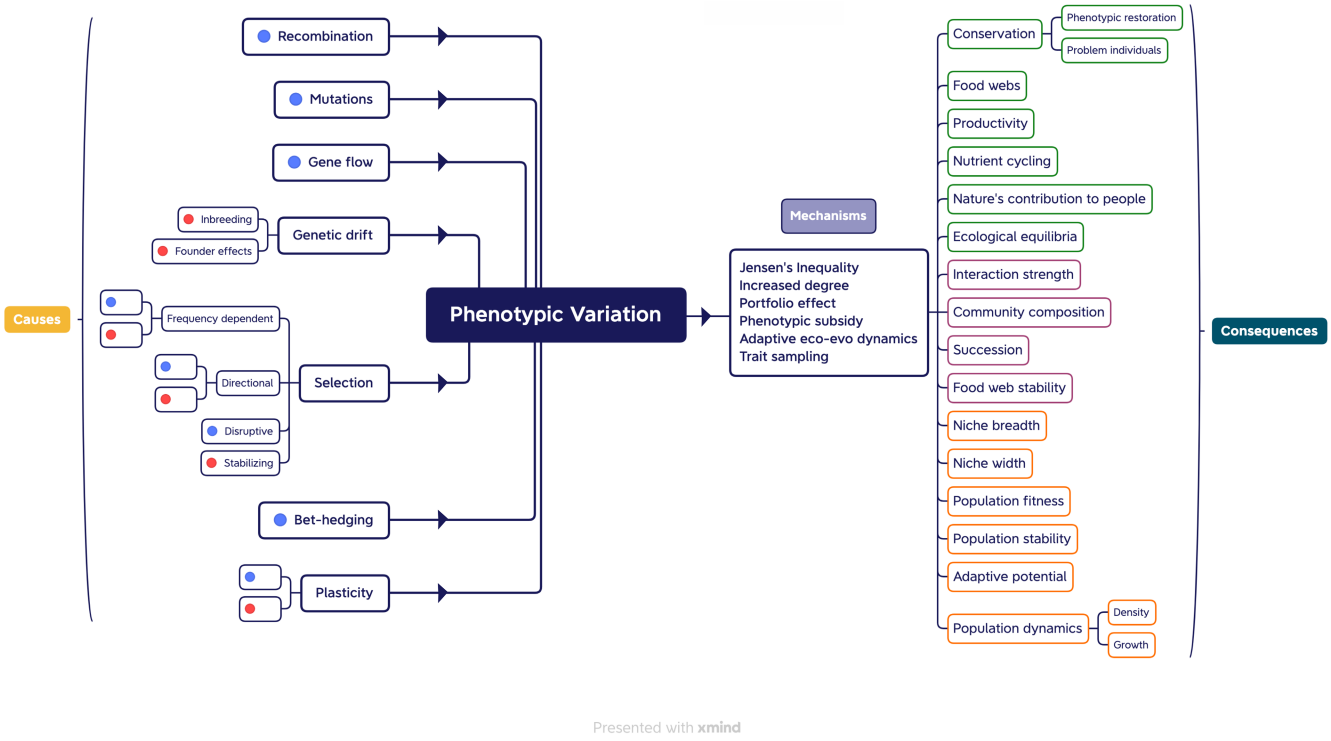

FIGURE 1 Conceptual figure depicting the causes (left) and consequences (right) of phenotypic variation within populations. Blue circles represent an increase in variation and red circles represent a decrease in variation. Concepts outlined in green represent consequences at the ecosystem level, in pink at the community level, and in orange at the population level. We note that all consequence could then feedback to influence all causes, but these arrows have been excluded for clarity. Refer to Bolnick et al. (2011) for detailed explanations of the mechanisms.

emigration (Figure 1; Brooks, 2002; Bolnick et al., 2003; Hansen et al., 2006; Hendry et al., 2018). Further, different types of selection are expected to shape phenotypic variation in different ways: stabilising selection should reduce variation, whereas disruptive selection, negative frequency-dependent selection and bet-hedging should increase variation (Figure 1; Bolnick & Ballare, 2020; Bolnick & Lau, 2008; Bull, 1987; Simons, 2011; Thompson et al., 2022; Van Valen, 1965). Finally, variation can be shaped by a diversity of interactions between genotypes and the environment (G × E), such as when spatial environmental variation inflates phenotypic variation across a given set of genotypes (Saltz et al., 2018). Importantly, all of these processes are expected to be strongly modified by various types of human disturbance (Palumbi, 2001; Somers et al., 2002; Vitousek et al., 1997), such as when pollution increases mutation, habitat loss decreases population size (increases drift) and reduces connectivity (decreases gene flow), and environmental stress induces new phenotypes.

Then, in turn, these contemporary changes in trait variation are expected to modify (evo-to-eco) population dynamics, community structure and ecosystem function—as well as ecosystem services and nature's contributions to people (Figure 1; Brunner et al., 2019; Hendry, 2017; Stange et al., 2021). The specific mechanisms of such effects are expected to include Jensen's inequality, increased degree, portfolio effect, phenotypic subsidy, adaptive eco-evo dynamics and trait sampling (see Bolnick et al., 2011 for details). Indeed, some of these effects have been demonstrated in 'community genetics' experiments that manipulate genetic or phenotypic variation (Hersch-Green et al., 2011). As examples, experimental treatments with greater intra-population diversity can show higher productivity or diversity (Agrawal et al., 2013; Johnson et al., 2006) and greater resistance to disturbance (Reusch et al., 2005) or invasive species (Hughes & Stachowicz, 2004).

In short, we ignore changes in variation to our peril and, indeed, several studies have emphasised (Mimura et al., 2017) or examined (Leigh et al., 2019) changes in within-population *genetic* variation. To our knowledge, however, no study has summarised changes in *phenotypic* variation in contemporary populations. Therefore, just as quantitative reviews and meta-analyses have galvanised and motivated studies on the eco-evolutionary dynamics of trait means (Alberti et al., 2017; Gorné & Díaz, 2019; Hendry et al., 2008; Sanderson et al., 2021), we feel that a similar development is needed for trait variation. That is our goal in the present paper. Specifically, we use a large database of Phenotypic Rates of Change in Ecology and Evolution (PROCEED—https://proceeddatabase.weebly.com) to ask questions relating to changes in trait variance in contemporary populations. Here, we ask (1) How do changes in trait variances compare to changes in trait

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means? (2) Do different human disturbances (Box S1) have different effects on trait variance? (3) Do different trait types (Box S2) have different effects on trait variance? (4) Do studies that established a genetic basis for trait change show different patterns from those that did not? We close by discussing the implication of our findings, the limitations of PROCEED, and provide recommendations for how to integrate changes in phenotypic variation in eco-evolutionary studies.

MATERIALS AND METHODS

To assess how different types of human disturbance might affect trait variance in wild populations, we use PROCEED. Since its last publication (Sanderson et al., 2021), the database has been significantly expanded from 7425 to 9222 entries, 336 to 425 species, 1664 to 1798 systems and 214 to 322 studies. The dataset used for our analyses consisted of 4507 effect sizes from 196 studies, 1431 systems and 177 species. This newer version of the database has some noteworthy changes compared to the earlier version of the database (see Sanderson et al., 2021): the addition of 1797 data points, the refinement and addition of trait types, and the clarification of data transformation. We note that 38.74% of the entries in the database use methods that reveal a genetic basis for trait differences (e.g. common gardens or quantitative genetic models), whereas the remainder cannot distinguish between heritable and plastic contributions.

We first describe some processes common to all analyses. First, all statistical analyses were performed in R environment version 4.2.1 (R Core Team, 2022). Second, we only use studies that were conducted in nature (i.e., non-experimental studies), that were of 300 generations or fewer since we are interested in assessing *contemporary populations* (Hendry et al., 2008), and that use ratio scale data because our effect sizes can only be calculated using measures truly bounded by zero (Nakagawa et al., 2015). Third, we include studies that have an allochronic (same population at different time points) or synchronic (populations with known divergence time) design. For synchronic studies, we only use entries where the first sample is known to be from the ancestral population. Finally, our analyses are limited to studies that provide a measure or means of estimating variances (i.e. standard deviation).

To answer each of our questions, we calculated two types of effect size measures using the 'escalc' function from the 'metafor' package version 3.8.1 (Viechtbauer, 2010): response ratios (lnRR) to assess changes in trait means and coefficient of variation ratios (lnCVR) to assess changes in trait variance and their corresponding sampling error variances (Hedges et al., 1999; Nakagawa et al., 2015). The response ratio, commonly used in ecology and evolution, is the natural logarithm of the ratio between two means (Hedges et al., 1999). The coefficient of variation ratio is the natural logarithm of the ratio between coefficient of variation for two groups (Nakagawa et al., 2015; Senior et al., 2020) which is an established effect size for measuring variance differences while accounting for changes in the mean (Sánchez-Tójar et al., 2020). We also use variability ratios (lnVR) when directly comparing changes in variation to changes in means because lnCVR takes into account changes in means.

Addressing the questions posed in the introductions starts with a qualitative assessment of data distributions, which is useful for inferences about what is typical and what is possible. These qualitative assessments were supplemented with formal statistical models that assess the importance of different potential moderators (e.g. predictors). Here, we performed analyses of lnRR and lnCVR using linear mixed effect meta-analytical models with the 'rma.mv' function in the 'metafor' package. We included effect size ID, study ID and system ID nested within species (phylogenetic relatedness correlation matrix) as random effects in our models to account for non-independence. We searched for species in the Open Tree Taxonomy (Rees & Cranston, 2017) and built the phylogenetic relationships using the Open Tree of Life (Hinchliff et al., 2015) in the 'rotl' package version 3.0.12 (Michonneau et al., 2016). Branch length was estimated using the 'compute.brlen' function from the 'ape' package version 5.6.2 (Paradis & Schliep, 2019). We resolved polytomies through randomisation using the 'multi2si' function from the 'ape' package.

To assess different moderators, we performed model selection using maximum likelihood method and the Akaike information criterion (AIC) for both effect response variables (lnCVR and lnRR) (Tables S1 and S2). We tested four moderators: data type (linear, area, cube, count, proportion, time, rate or other), design (allochronic or synchronic), data transformation (if the means and standard deviation were computed based on transformed data), and number of generations (the number of generations elapsed given the number of years elapsed for a given system). For lnCVR, the model with the lowest AIC value included effect size ID, study ID and system ID nested within species (phylogeny) as random effects and data transformation and generations as moderators. For lnRR, the model with the lowest AIC value included the same random structure and data transformation, generations and design as moderators.

We then ran the best fitted model using a restricted maximum likelihood method to estimate the coefficients and our three moderators of interest (Tables S3–S7): disturbance (climate change, harvesting, introductions, pollution, landscape change, response to introductions or other), trait type (phenology, behaviour, physiology, growth, size, morphology, life history or responses) and genphen (genetic or phenotypic studies). For both the lnCVR and lnRR models, the test for residual heterogeneity was significant ($p<0.0001$). For lnCVR the test

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of moderators was non-significant ($p = 0.2451$) but was significant ($p < 0.0001$) for lnRR.

To further assess how changes in variances compare to changes in means, we ran a model where lnVR (Tables S8 and S9) was the response variable and moderators were generations, data transformation, design, trait type, and an interaction between disturbance and lnRR. We included the same random structure as described above. We note that we use lnVR here, rather than lnCVR, since lnCVR take into account changes in means (Hedges & Nowell, 1995).

RESULTS AND DISCUSSION

Our database reveals that changes in phenotypic variation within populations are typically small, albeit with some instances of very large change (Figure 2; Figure S1). This overall 'many-small/few-large' pattern is similar to those documented for compilations of phenotypic selection (Kingsolver et al., 2001; Siepielski et al., 2009, 2013), changes in mean trait values (Hendry et al., 2008; Kinnison & Hendry, 2001; Sanderson et al., 2021), and additive genetic variance in fitness (Bonnet et al., 2022; Hendry et al., 2018). The likely general explanation for these analogous patterns across evolutionary parameters is that most studied populations are reasonably well adapted for their local environments (Haller & Hendry, 2014; Hendry, 2017), whereas a smaller set of populations are facing large environmental perturbations that render them maladapted, under strong selection and evolving rapidly (Brady et al., 2019).

The general stability of trait variance within populations (75% of cases showed less than 1.21% change in the coefficient of variation) confirms the expectation of a typical balance between factors that increase and decrease variation (Figure 1). On the one hand, phenotypic variation is expected to increase due to a variety of non-adaptive processes (Figure 1; e.g. mutations and developmental noise), as well as some adaptive processes (Figure 1; e.g. disruptive selection, negative frequency-dependent selection and bet-hedging). Any resulting increases in phenotypic variation are then expected to be counterbalanced by directional and stabilising selection that remove maladaptive variation through the elimination of individuals that deviate most from the phenotypic optimum (Figure 1; Haller & Hendry, 2014). Further, selection on genotype-by-environment interactions could buffer against environmental change and therefore maintain existing levels of variation (Bulmer, 1971). Our results confirm that the two sides of this equation are typically close to some sort of equilibrium, at least over the time scales considered here. As a specific example, purple Loosestrife introduced to North America showed essentially no change in variation in the number of branches over a 200-year time span (Chun et al., 2007).

Despite the overall stability of phenotypic variation in most populations, some instances of noteworthy increases or decreases were found. For example, 1% of the cases showed greater than 5% change in within-population coefficient of variations. Some dramatic examples of *decreasing* phenotypic variation include the body size of juvenile Atlantic cod subject to intensive fishing along the Norwegian coast (Olsen et al., 2009), body length in European grayling introduced to Norwegian lakes (Haugen & Vøllestad, 2001), and development time in soapberry bugs colonising a new host plant in Florida (Carroll et al., 1997). Some dramatic examples of *increasing* phenotypic variation include the concentration of pyrrolizidine alkaloids in stinking willie introduced to North America (Stastny et al., 2005), skull length in small Indian mongoose introduced to Pacific islands (Simberloff et al., 2000), and body length in threespine stickleback naturally colonising a lake in Alaska (Baker et al., 2019). In short, striking examples were observed of changes in both directions and, indeed, we did not observe any overall general bias toward increasing or decreasing variance (Figure 2; Figure S1).

The absence of a 'typical' direction (increase or decrease) of change in phenotypic variation likely reflects context-specific changes in the various factors causing increases and decreases in variation. In short, the lack of a significant 'average' effect in our statistical models should not be interpreted as a *lack* of change, but rather as a great variety of changes (from large to small and from negative to positive) that vary among populations and traits. The largest of these changes clearly have the scope to shape large ecological consequences (e.g. see table S1 in Wennersten & Forsman, 2012). Even modest changes in variance could have important ecological consequences—as has been demonstrated via experiments that manipulate within-species variation (Ingram et al., 2011; Post et al., 2008; Schweitzer et al., 2008). With this background, we can now consider the four questions posed at the outset of our paper.

(1) How do changes in trait variances compare to changes in trait means?

Many studies have emphasised the eco-to-evo and evo-to-eco importance of changes in mean trait values—that is, the first moment of the phenotypic distribution—for evolution and ecology (Darimont et al., 2009; Hendry et al., 2008; Sanderson et al., 2021). Our analysis suggests that changes in trait variation are not smaller (overall) than are changes in trait means (Figures 2 and 3). Thus, we should not ignore the second moment of the distribution. Although distributions of change were not significantly different from zero for either moment (because most values were small and because increases and decreases were roughly similar in number), we do suggest one important

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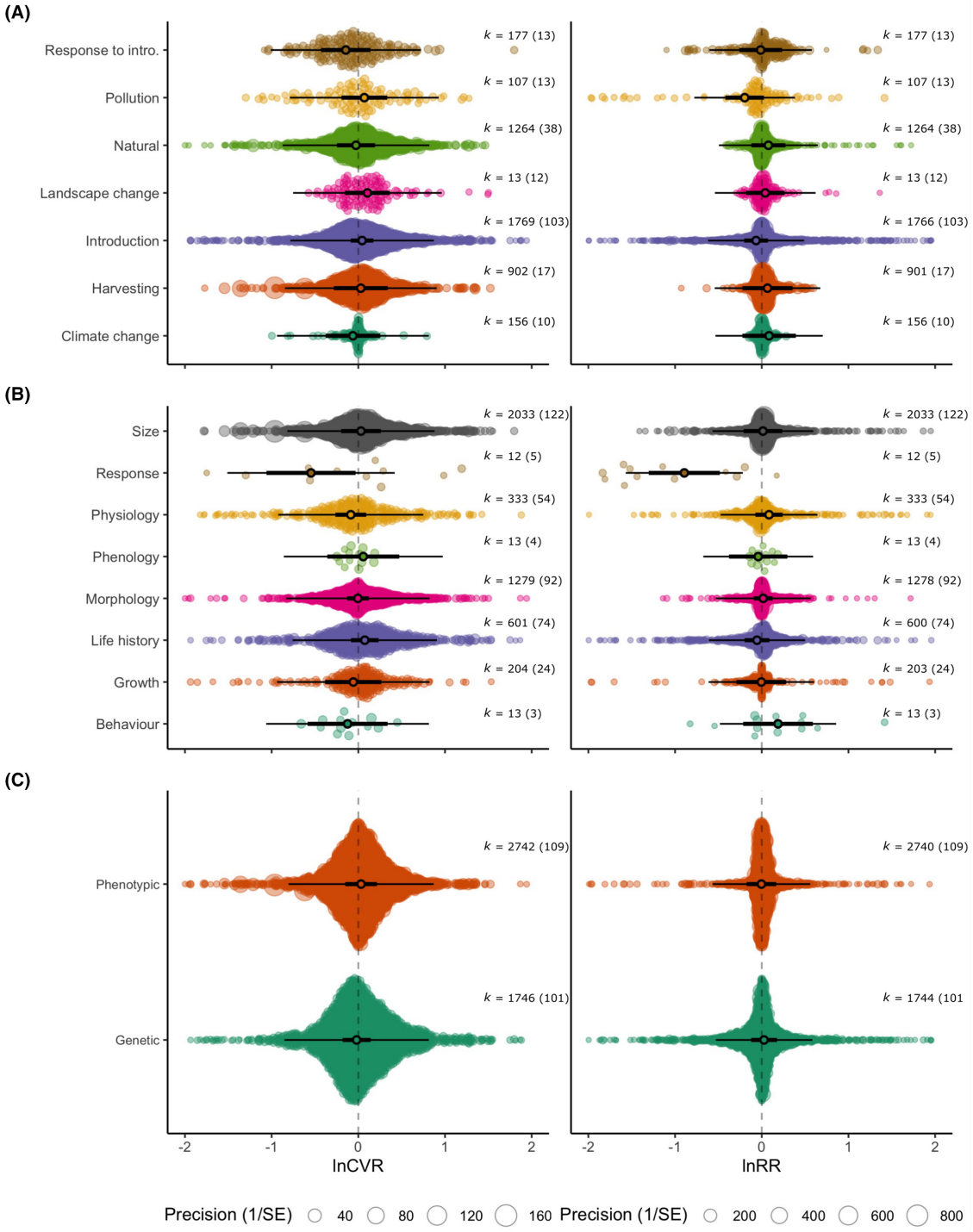

FIGURE 2 Orchard plot depicting meta-analytic results of coefficients of variation. Circles represent individual effect sizes, bold bars represent confidence intervals, bars represent prediction intervals, and bold circles represent point estimates. Axes have been cut to improve data visualisation (see Figure S1 for all data points). Panels (a) compare different types of human disturbance, panels (b) compare different types of traits and panels (c) compare genetic and phenotypic studies.

potential difference. Specifically, the lnCVR (changes in variation) distributions appear to be more platykurtic (kurtosis = 11.56) than were the lnRRs (changes in means) distributions (kurtosis = 32.44) (Figure 2). If this result holds under further scrutiny, it suggests that extreme changes might be more important for means than for variances, but that more typical changes (irrespective of direction) might be more important for variances than for means.

We can go further than a comparison of these overall distributions—because each study in our database has measures of change in both moments. We first

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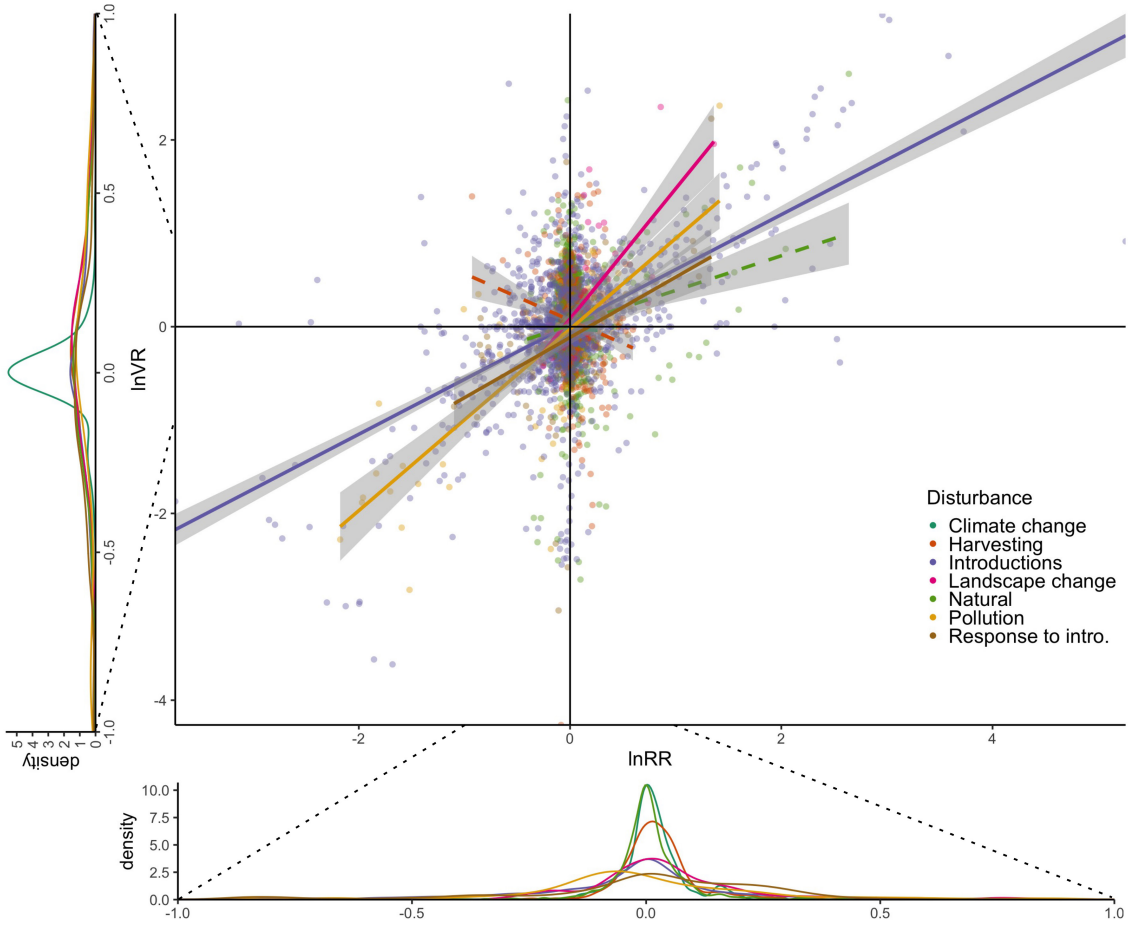

FIGURE 3 Variation ratios (lnVR) as a function of response ratios (lnRR). Note that we use lnVR here (as opposed to lnCVR) because lnCVR take into account changes in means. Data are coloured by type of human disturbance. Solid lines are significant and dashed lines are non-significant regressions from a model where the response variable is lnVR, generations, data transformation, study design, trait type and disturbance lnRR interaction are moderators, and effect size ID, system ID nested within species (phylogeny), reference ID as random effects. The data distributions are plotted outside each of the axes, with the axes truncated for better visualisation on the density plots.

might expect that changes in selection would lead to a particular correspondence in the two responses: for instance, stabilising selection should either decrease or increase the mean but should (in both cases) decrease the variance (Figure 1). In fact, for certain types of human disturbance (p = 0.0007, introductions; p = 0.0012, landscape change; p = 0.0007; and p = 0.0007, response to introduction), we found a correlation between changes in variation (here, lnVR) and changes in mean (lnRR) (Figure 3; Tables S8 and S9). Moreover, some studies show decreases in variance but no change in means, which could suggest (for example) a decrease in developmental noise or an increase in stabilising selection. One such case appears to be thorax width in soapberry bugs introduced into Florida (Carroll et al., 1997). Other studies show increases in variance but no change in means, which could suggest (for example) an increase in disruptive selection or developmental noise, such as Chum salmon body length in Alaska (Oke et al., 2020). Direct measures of selection on such populations could help to tease out these potential alternatives.

(2) Do different human disturbances have different effects on trait variance?

We did not find any obvious differences between types of human disturbance in their effects on changes in either mean trait value or trait variance (Figure 2; Figure S1; Tables S2 and S5). In other words, no disturbance types caused noteworthy 'stand-out' effects on either moment (mean or variance) of phenotypic distributions (Tables S4 and S6). However, this *statistical* non-result should not be taken as a *biological* non-result. The reason is that each type of human disturbance sometimes caused large changes in one or both moments, but were about as frequently positive as they were negative. Stated another way, every disturbance type often had no effect on means or variation; yet sometimes substantially increased and other times substantially decreased means or variation (Figure 2). Note also that the lack of differences between disturbance types for changes in mean trait values does not necessarily contradict previous findings (Darimont et al., 2009; Hendry et al., 2008; Sanderson et al., 2021)

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because we are here considering the direction of change rather than the absolute magnitude of change (as in previous work).

Despite this general similarity across the different types of human disturbance, we feel it is valuable to speculate on a few of the suggestive trends that would benefit from consideration in future work. For instance, 62% of the data for responses to introductions showed a decrease in variation, which reinforces suggestions that introduced species generally impose strong selection on native species toward new phenotypic optima, which could decrease variation (Figure 1; Kim et al., 2003; Strauss et al., 2006). A similar, but weaker, trend was suggested for climate change (57% of the data showed a decrease in variance)—and perhaps for the same reasons of expected directional selection (Logan et al., 2014; Marrot et al., 2018). On the other hand, 58% of the data for responses to landscape changes suggested an increase in variance, although we do not have a clear rationale for why such a pattern might arise. Of course, we reiterate that these suggestions are based on non-significant 'trends', probably because of massive heterogeneity in response to each disturbance type.

(3) Do different trait types have different effects on trait variance?

Different trait types are expected to have different evolutionary and ecological properties and, as such, have been the subject of comparative analyses that test for differences in selection (Kingsolver et al., 2001; Kingsolver & Diamond, 2011), heritability (Mousseau & Roff, 1987), evolvability (Houle, 1992), developmental instability (Hansen et al., 2006) or changes in mean phenotype (Kinnison & Hendry, 2001). In this comparative spirit, we asked if different trait types show different patterns of change in phenotypic variation. As was the case for different types of human disturbance (see above), no trait types showed changes in variance that were significantly different from zero. Instead, all trait types sometimes showed positive and sometimes negative changes in trait variation, and most of those changes were small but some were large. The potential reasons for this general pattern were described above.

Again, it seems worthwhile and interesting to speculate on suggestive trends. In particular, decreases in variance might be more common for response traits (e.g. plant size) and behaviour traits (e.g. time spent foraging, predator escape speed, flight initiation distance). For both types of traits, a decrease in variance might imply strong stabilising selection on aspects of performance—and that such selection increases under environmental change. In both cases, however, sample sizes were small and we defer additional speculation until more data have accumulated. Regardless of any such potential trends in variance change, we reiterate that each type of trait showed some instances of large decreases and other cases of large increases. As an example of the former, body size in Alaskan chum salmon showed a large decrease in variation (Clark et al., 2018; Oke et al., 2020). As an example of the latter, the total concentration of alkaloids in stinking willie showed a large increase in variation (Stastny et al., 2005).

(4) Do studies that established a genetic basis for trait change show different patterns from those that did not?

Many studies have discussed the relative contributions of genetic and environmental effects to contemporary changes in mean phenotype (Anderson et al., 2014; Merilä & Hendry, 2014; Wong & Candolin, 2015). In some cases, quantitative genetic analyses or common garden experiments are sufficient to assign a genetic or plastic basis to changes in traits—or to partition the contributions from each source. In most cases, however, genetic versus plastic contributions to phenotypic changes are unknown. Previous comparative analyses of contemporary changes in trait means have been saddled with this uncertainty, and have attempted a partial solution by comparing the overall distribution of changes to the distribution for studies where a genetic basis has been confirmed (Hendry et al., 2008; Sanderson et al., 2021). These crude comparisons have revealed that the largest phenotypic changes tend to occur in studies that have not confirmed a genetic basis, suggesting a particularly large contribution from plasticity. Of course, it should be noted that 'genetic' studies do sometimes reveal large changes, and that genetic changes might be large even in studies that cannot confirm it.

The genetic versus plastic contributions to changes in trait variance are even harder to partition; and, hence, few studies of natural populations have tried to establish the contemporary evolution (as opposed to plasticity) of changes in phenotypic variation. Here, we provide a crude starting point by comparing changes in trait variation between studies where the changes in trait means are known to be genetically based (as opposed to not known). Overall, the distributions of effect sizes (lnRR and lnCVR) are very similar for the two types of studies, which suggests—albeit imperfectly—that changes in phenotypic variation probably do sometimes have a genetic basis (Figure 2). For example, soapberry bugs colonising a new host in Florida showed a large decrease in variation in development time, for which the study confirmed a genetic basis for changes in trait means (Carroll et al., 1997). Further insight requires that more studies examine, when possible, the genetic contributions to contemporary changes in phenotypic variation.

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Limitations and extensions

PROCEED comes with limitations that need to be appreciated. First, as mentioned above, relatively few studies assign a genetic versus plastic contribution to changes in trait means (Merilä & Hendry, 2014), and this shortcoming is even greater for changes in trait variation. We therefore encourage the continued proliferation of study approaches (e.g. animal models or common garden experiments) that can estimate genetic contributions to trait change. Second, although the database captures an incredible diversity of systems, populations, traits, and species, the diversity of entries remains unbalanced (Table S3), with some very small sample sizes that limit inferences. Finally, we suspect an ascertainment bias where researchers tend to focus on populations known to be experiencing influential human disturbances. This ascertainment bias would tend to increase effect sizes—although the second contribution presumably affects means more than variances. Similarly, we suspect an 'invisible fraction' of sorts where human disturbances cause extinction of some populations which therefore would not be represented in our database. For trait means, it remains unclear how these extinction events might bias compilations of changes in mean trait values (Hendry et al., 2008). For variances, we suggest a bias against large decreases simply because unmeasured populations that declined to extinction (and are therefore missing from the database) might show the largest declines in phenotypic variation—although recent studies suggest that even very small populations do not always have low phenotypic variation (Wood et al., 2015).

We recommend the use of time series data in future analyses to observe some of the patterns suggested above in finer resolution. For instance, Olsen et al. (2009) found no change in mean juvenile size across 90 years in Norwegian Atlantic Cod, but a steady decrease in variation in size across this same time period. Such time series can help find the causes of different changes in variance and better test corresponding hypotheses. We might expect more rapid variance changes closer to the start of a human disturbance, as opposed to after the population adapts (if it does) to its new environment. As an alternative hypothesis, in cases where human disturbances cause dramatic population declines, we might expect phenotypic variance to decline only when the population gets very small (but see Vignon et al., 2023). In Box 1, we further develop examples of profitable questions to be examined.

Implications

Our study suggests that, although phenotypic variation does not change consistently across traits and

BOX 1 Some questions that can motivate future work on contemporary changes in phenotypic trait variance—using the PROCEED database and other approaches.

1. How do mean trait values and variances change in relation to estimated strength of selection?
2. How do mean trait values and variances change in relation to environmental heterogeneity?
3. How much do changes in variance reflect trimming or expansion of one tail of a trait distribution versus both tails (which might reflect differences between directional and stabilising selection)?
4. What can time series (as opposed to the present end-point comparisons) tell us about the tempo and mode of variance change? Are estimates of variance change subject to temporal scaling? Does most change in variance happen right after a perturbation and by what degree?
5. How do inferences change in methods (e.g. Bayesian) that formally account for uncertainty—given that uncertainty in trait measurements will upwardly bias estimates of trait variance?
6. How strongly and directly do increases or decreases of trait variance map onto changes in ecology and how does this compare with changes in trait means?
7. What is the null (drift) expectation for variation change in populations not facing selection, and is it possible to identify non-null outcomes beyond which change was likely due to (for example) selection or gene flow?
8. How will different mechanisms (e.g. Jensen's inequality, increased degree, portfolio effect, phenotypic subsidy, adaptive eco-evo dynamics, and trait sampling) respond to changes in phenotypic variation?
9. Can we ascribe particular ecological effects to observed changes in variation—as was done, for example, by Oke et al. (2020) for changes in trait means?
10. How will inferences about effects of human disturbance change if we ignore the direction (positive or negative) of changes in variance, as we have done here, and instead examine the magnitude (e.g. absolute value) of change?

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disturbances, investigators do sometimes see large increases or decreases (eco-to-evo), which could have substantial ecological consequences (evo-to-eco). The synergistic and counteractive processes that shape phenotypic variation within populations (Figure 1) make it difficult to predict how variation within a population might change—yet the consequences of either could be severe. In particular, intraspecific trait variation is known to have important implications not only for population dynamics, but also for species interactions, communities, and ecosystem processes (Thompson et al., 2022).

In short, although comparative analyses such as ours can reveal the variation in responses, it is most important to consider the specific individual responses of particular traits in particular populations of particular species. A few examples will serve to illustrate this point. First, high variation can buffer against environmental fluctuations including those caused by humans, such as through portfolio effects (Schindler et al., 2010). Second, high phenotypic variation linked to niche differentiation or range expansions can lead to the exclusion of inferior competitors (Barabás & D'Andrea, 2016). Third, changes in intraspecific variation can also have effects on ecological processes such as pollination or seed dispersal.

For these reasons, we encourage future work to explicitly incorporate changes in phenotypic variation into eco-evolutionary studies. Many studies already have a measure of variance for their study population, and we therefore encourage their publication and comparison with other studies. Further, to the many studies calling for the monitoring of genetic variation (Leigh et al., 2019; Mimura et al., 2017), we add calls for the monitoring of phenotypic variation. After all, phenotypic (as opposed to genetic) variation is the nexus through which organisms interact with their environments.

AUTHOR CONTRIBUTIONS

Sarah Sanderson, Michael T. Kinnison, Rose E. O'Dea, Lucas D. Gorné, Andrew P. Hendry and Kiyoko M. Gotanda contributed to data collection. Sarah Sanderson, Daniel I. Bolnick, Michael T. Kinnison, Andrew P. Hendry and Kiyoko M. Gotanda designed the study. Sarah Sanderson performed the analyses with support from Lucas D. Gorné and Rose E. O'Dea. Sarah Sanderson wrote the first draft of the MS and all authors contributed significantly.

ACKNOWLEDGEMENTS

This work has been supported by an NSERC Discovery Grant and Tier 1 Canada Research Chair (APH), the Faculty of Mathematics and Science at Brock University (KMG & LDG), NSF IOS-2222339 (MTK), NSF OIA-1849227 (MTK), Maine Agricultural and Forest Experiment Station (USDA) (MTK), and by NSERC CGS-D (Canada Graduate Scholarships Doctoral Program) 569441-2022 (SS). 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 6.0. We are especially grateful to both the Carnegie Museum of Natural History and the Powdermill Avian Research Centre for sharing their data.

FUNDING INFORMATION

Faculty of Mathematics and Science at Brock University; Marine Agricultural and Forest Experiment Station; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: 569441-2022; Office of Integrative Activities, Grant/Award Number: 18492272222339.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.14186.

DATA AVAILABILITY STATEMENT

The data supporting our results is archived at https://doi.org/10.5683/SP3/NXSL3Q, and can be found on the PROCEED website (https://proceeddatabase.weebly.com).

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SUPPORTING INFORMATION

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How to cite this article: Sanderson, S., Bolnick, D.I., Kinnison, M.T., O'Dea, R.E., Gorné, L.D., Hendry, A.P. et al. (2023) Contemporary changes in phenotypic variation, and the potential consequences for eco-evolutionary dynamics. *Ecology Letters*, 26(Suppl. 1), S127–S139. Available from: https://doi.org/10.1111/ele.14186

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