

The evolution of phenotypic plasticity in response to anthropogenic disturbance

Erika Crispo¹, Joseph D. DiBattista¹, Cristián Correa¹,
Xavier Thibert-Plante¹, Ann E. McKellar², Amy K. Schwartz¹,
Daniel Berner³, Luis F. De León¹,
and Andrew P. Hendry¹

¹Department of Biology and Redpath Museum, McGill University, Montreal, Quebec, Canada,

²Department of Biology, Queen's University, Kingston, Ontario, Canada and

³Zoological Institute, University of Basel, Basel, Switzerland

ABSTRACT

Questions: Do evolutionary changes in phenotypic plasticity occur after anthropogenic disturbance? Do these changes tend to be increases or decreases in plasticity? How do these evolutionary patterns differ among taxa and trait types? Does evolution of plasticity change with time since the disturbance?

Data incorporated: Evolutionary rates for plasticity estimated from 20 studies that have compared a plastic response in two or more populations, at least one of which had experienced an anthropogenic disturbance in nature and at least one of which had not.

Method of analysis: We estimate evolutionary rates (darwins and haldanes) for plasticity for each study, which represent the amount of evolutionary change in plasticity. We then perform analyses of covariance, with the evolutionary rate numerator (amount of evolutionary change) as a response variable, taxa and trait type as predictor variables, and the amount of evolutionary time as a covariate.

Conclusions: We find that plasticity has evolved in several cases, including both increases and decreases in the levels of plasticity following anthropogenic disturbances. The typical direction of this evolutionary response depends on an interaction between taxon and trait type. For instance, invertebrates sometimes show the evolution of *increased* plasticity for life-history traits, but the evolution of *decreased* plasticity for morphological traits. Plants, on the other hand, show no trends in the direction of plasticity evolution.

Keywords: adaptation, adaptive plasticity, climate change, contemporary evolution, human impact, meta-analysis, rapid evolution, reaction norms.

Correspondence: E. Crispo, Department of Biology and Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec H3A 2K6, Canada. e-mail: erika.crispo@mail.mcgill.ca
Consult the copyright statement on the inside front cover for non-commercial copying policies.

INTRODUCTION

Human impacts on the environment are increasingly problematic for the persistence of populations and species. These anthropogenic influences might be particularly detrimental to population persistence, in comparison with more natural environmental changes. Possible reasons include that anthropogenic disturbances can often cause more rapid environmental changes (e.g. Vitousek *et al.*, 1997; Petrin *et al.*, 2008) and can involve novel stressors [i.e. those to which organisms have not been exposed during their evolutionary history (e.g. Macnair, 1991)]. In short, environmental changes in general, and anthropogenic influences in particular, should cause populations to become maladapted to their local environments. This maladaptation might then cause population declines and perhaps extinction (Maynard Smith, 1989; Bürger and Lynch, 1995; Gomulkiewicz and Holt, 1995). A recourse that organisms have is to respond adaptively to the environmental change, thus increasing fitness, population size, and the probability of persistence.

Studies of adaptive responses to environmental change have traditionally focused on how natural selection influences the non-plastic components of traits (e.g. Bumpus, 1899; Cain and Sheppard, 1954; Kettlewell, 1958; Antonovics and Bradshaw, 1970; Bürger and Lynch, 1995; Gomulkiewicz and Holt, 1995; Orr and Unckless, 2008). More recently, increasing attention has been paid to the role of phenotypic plasticity (for reviews, see Price *et al.*, 2003; Crispo, 2007; Ghalambor *et al.*, 2007; Carroll, 2008; Gienapp *et al.*, 2008). Phenotypic plasticity is defined as environmentally induced changes in the phenotype of an individual organism. In some cases, phenotypic plasticity might be adaptive, allowing individuals to ‘jump’ from one fitness peak to another, without traversing fitness valleys (Price *et al.*, 2003; Crispo, 2007; Ghalambor *et al.*, 2007). Supporting this idea, a quantitative review of phenotypic change in natural animal populations has invoked a role for plasticity in facilitating phenotypic responses in disturbed populations (Hendry *et al.*, 2008). It is also true, however, that plastic responses are sometimes maladaptive (see below). The consequences of plasticity for fitness under environmental change are therefore not straightforward.

Considering that plastic responses can have fitness consequences, it is intuitive that plasticity can be subject to selection and might therefore evolve (e.g. Hairston and De Meester, 2008; Zou *et al.*, 2009). The evolution of plasticity will require at least two basic components. The first is genetic variation in plasticity [i.e. genotype \times environment interactions (Via and Lande, 1985; Scheiner, 1993)]. Several studies have shown that such variation is indeed often present in natural populations (e.g. Danielson-François *et al.*, 2006; Chun *et al.*, 2007; Etges *et al.*, 2007; Hutchings *et al.*, 2007; Nussey *et al.*, 2007; but see Charmantier *et al.*, 2008). The second component is a correlation between plasticity and fitness. Note that plasticity can influence fitness directly, if the ability to be plastic is adaptive/maladaptive, such as when environments vary on small spatial scales or short time scales (Padilla and Adolph, 1996; Sultan and Spencer, 2002; Crispo, 2008; Stomp *et al.*, 2008). Alternatively, plasticity can influence fitness indirectly, if the phenotype produced via the plastic response is adaptive/maladaptive (Via *et al.*, 1995). Correlations between plasticity *itself* and fitness (e.g. Steinger *et al.*, 2003), or between a particular plastic *response* and fitness (e.g. Donohue *et al.*, 2000), have also been documented in nature.

Adaptive versus maladaptive plasticity

Increases in plasticity might evolve if plasticity itself is adaptive, such as when environments fluctuate temporally or spatially (Padilla and Adolph, 1996; Alpert and Simms, 2002; Sultan and Spencer, 2002; Crispo, 2008; Stomp *et al.*, 2008). Selection on plasticity might be more likely to occur when

plasticity is reversible/labile than when it is irreversible/developmental (Alpert and Simms, 2002; Gabriel, 2006). Alternatively, if the most plastic individuals express the most extreme phenotypes, increased plasticity might evolve as a by-product of selection on the most extreme phenotypes (Via *et al.*, 1995). For example, increased plasticity in inter-node length and flowering time in *Impatiens capensis* plants from sunny sites, relative to those from closed-canopy sites, is a result of selection on trait values rather than on the plasticity of these traits (Donohue *et al.*, 2000). This was determined by comparing fitness to both the level of plasticity of a given genotype and the genotype's mean phenotype – although plasticity and the phenotypic values were correlated, fitness was more strongly associated with phenotypic values (Donohue *et al.*, 2000). Regardless of how selection acts on plasticity, if plasticity increases fitness following anthropogenic disturbance, we would expect that increased levels of plasticity might evolve.

On the other hand, plastic responses might be maladaptive in a new environment, and in these cases decreased plasticity might evolve. Maladaptive plastic responses might be particularly likely under novel conditions resulting from anthropogenic disturbances, because organisms might not have experienced similar selection pressures during their evolutionary histories. In this case, mechanisms for sensing and responding adaptively to specific environmental cues might not have evolved (Ghalambor *et al.*, 2007). Alternately, the plastic *response* might be adaptive, but plasticity *itself* might still be maladaptive because the costs of plasticity outweigh its benefits (DeWitt *et al.*, 1998; Van Buskirk and Steiner, 2009). As an example, snails (*Physella virgata*) respond to the presence of both native molluscivorous fishes and foreign non-molluscivorous fishes by plastically increasing shell thickness. However, plasticity is not adaptive in the latter context, and might actually be maladaptive due to associated growth costs (Langerhans and DeWitt, 2002). Under such conditions, when the costs of plasticity outweigh its potential benefits, we might expect evolutionary decreases in plasticity.

Factors influencing the evolution of plasticity

Different taxa might show different evolutionary changes in plasticity following anthropogenic disturbance. Animals, for instance, can more effectively use behavioural plasticity as an adaptive response to changing environmental conditions than can plants. As one example, many animals can disperse to areas in which their phenotypic traits are better suited for prevailing environmental conditions (Edelaar *et al.*, 2008; Clobert *et al.*, 2009). Plants, in contrast, have a much lower potential for this type of plasticity. One possibility is that the more sedentary nature of plants might increase their relative exposure to overall environmental degradation, which could in turn increase the potential for maladaptive plasticity and thereby promote the evolution of reduced plasticity (Alpert and Simms, 2002; van Kleunen and Fischer, 2005). Another possibility is that the reduced importance of behavioural plasticity in plants might result in selection for increased levels of plasticity in other types of traits.

Different types of traits might also show different evolutionary changes in plasticity. First, some traits might respond more *rapidly*, meaning that the time lag between sensing an environmental cue and the resulting phenotypic response is shorter (Padilla and Adolph, 1996; Gabriel *et al.*, 2005; Stomp *et al.*, 2008). Examples of traits with particularly rapid responses include inter-node length and chemical defences in plants (for a review, see Alpert and Simms, 2002), behavioural traits in animals (see above), and physiological traits in general (e.g. Timmerman and Chapman, 2004; Seebacher, 2005; Caruso *et al.*, 2006). Given that a short time lag should most strongly

influence the adaptive value of plasticity (e.g. Gabriel, 2006; Stomp *et al.*, 2008), plasticity in such traits might be more likely to evolve after a disturbance. Second, some traits might show *stronger* plasticity, meaning that the magnitude of the plastic response in relation to a given environmental context is greater. For example, behavioural plasticity is greater than morphological plasticity in anurans exposed to predation pressure (Relyea, 2001). The strength of the plastic response might influence selection on plasticity, and thus increase the likelihood that plasticity will evolve following environmental change. Third, the heritability of plasticity probably differs among types of traits [as does the heritability of non-plastic components of traits (Mousseau and Roff, 1987; Houle, 1992; Stirling *et al.*, 2002)], which would also affect the likelihood of plasticity evolution.

Temporal trends

What temporal trajectories might be expected for plasticity evolution? First, plasticity could evolve as an immediate response – that is, over one or a few generations. This might occur when genetic variation for plasticity is quickly depleted through a selective sweep, or when the initial evolutionary change in plasticity achieves near-optimal levels (i.e. no additional selection for increased plasticity). In this case, we would expect a rapid evolutionary change in plasticity followed by little or no subsequent change. Second, plasticity could evolve more gradually, which might occur if the initial standing genetic variation for plasticity is low, or if the environment continues to change through time (Visser, 2008). An alternative is that plasticity might not evolve at all, particularly if genetic variation for plasticity is very low (e.g. Charmantier *et al.*, 2008), or if selection on plasticity does not differ between disturbed and undisturbed populations. Or plasticity might change unpredictably owing to gene flow between environments (Crispo, 2008) or genetic drift (Masel *et al.*, 2007). Genetic bottlenecks resulting from anthropogenic disturbances might make non-adaptive changes particularly prevalent. These contrasting possible trajectories have also been debated in the context of non-plastic trait components (e.g. Kinnison and Hendry, 2001; Schwartz and Karl, 2005; Estes and Arnold, 2007; Hendry *et al.*, 2008; Ahern *et al.*, 2009; Jacquemyn *et al.*, 2009).

Here, we use a meta-analytic approach to examine quantitatively some of the ideas detailed above. Specifically, we estimate evolutionary rates (darwins and haldanes) for plasticity from studies that raised multiple populations (disturbed and undisturbed) under multiple common-garden treatments. The numerators of these rates represent evolutionary change in plasticity. We then compare these metrics among taxa and trait types and test for changes in the evolution of plasticity with time. Our analyses inform how often, in what direction (increase or decrease in plasticity), in which taxa, for which traits, and how rapidly plasticity has evolved in nature.

METHODS

Insight into the evolution of plasticity following anthropogenic disturbance can be gained from studies that measure differences among populations in the plastic responses of traits. These studies include those that use common-garden experiments with multiple treatments (i.e. two or more ‘common-garden’ conditions) to assess plasticity for related populations that have or have not experienced an anthropogenic disturbance in nature. By ‘related’ populations we mean two or more populations that were recently founded from a common ancestral population, or that have known ancestor–descendent relationships. Because we

are interested in how rapidly plasticity evolved, we only consider studies in which the length of time since the anthropogenic disturbance is known.

Our database was initiated with four relevant studies from the database of Hendry *et al.* (2008): Carroll *et al.* (1997, 1998, 2005) and Trussell and Smith (2000). It was then expanded by an additional 16 suitable studies through keyword searches in the ISI Web of Science (keywords included ‘evolutionary change’, ‘rapid evolution’, ‘contemporary evolution’, ‘haldanes’, ‘darwins’, and ‘phenotypic change’) and through the Related Records option of the ISI Web of Science. All studies that met the criteria outlined in the preceding paragraph were included in the database. Eleven of the 20 studies examined species introduced into a new environment, five examined native species following the introduction of a foreign species, and four examined populations experiencing habitat degradation. For each study, we also recorded the time since the disturbance and the generation length of the species in question – this information was taken directly from the articles or was provided by the authors of the original papers.

Data on plasticity were obtained from tables or figures in the papers, or were provided by the authors of those papers. We extracted data from figures using DataThief III (version 1.1), which estimates the coordinates for data points within graphs. We calculated darwin numerators and, when possible, haldane numerators, which represent two complementary measures of evolutionary change (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001):

$$\text{darwin numerator: } (\ln |(X_1 - X_2)_d| - \ln |(X_1 - X_2)_u|)$$

$$\text{haldane numerator: } [(\ln |(X_1 - X_2)_d| - \ln |(X_1 - X_2)_u|)/CV_p]$$

where \ln is the natural logarithm, X is the mean trait value for a population raised in a common-garden treatment, subscripts 1 and 2 denote two different common-garden treatments, subscript d denotes the disturbed population (i.e. impacted by humans) and subscript u denotes the undisturbed population, CV is the coefficient of variation, and subscript p indicates pooled values. CV_p was calculated as follows:

$$SS = s^2(n - 1)$$

$$s_p^2 = (SS_d + SS_u)/(n_d + n_u - 2)$$

$$CV_p = s_p/[(|(X_1 - X_2)_d| + |(X_1 - X_2)_u|)/2]$$

where s^2 is the variance of the difference between two common-garden treatments for one population, SS is the sum of squares for this difference, n is the average sample size for each population, and subscripts are defined as above. The evolutionary rate numerators differ in that darwin numerators represent the proportional change in plasticity, whereas haldane numerators represent the change in plasticity standardized by variation in plasticity.

When multiple disturbed or undisturbed populations were examined in a study, we performed the above calculations for all possible pairwise comparisons between the two population types. The resulting data thus represent differences in plasticity for a particular trait in a particular comparison of disturbed and undisturbed populations within a particular study. A positive value for the darwin or haldane numerator indicates an evolutionary increase in plasticity following disturbance, whereas a negative value indicates an evolutionary decrease in plasticity. Our data set included a total of 381 darwin numerators and 333 haldane numerators. No evidence of publication bias was observed in the data set – that is, studies with a combination of low sample sizes and low levels

of plasticity were not under-represented (analyses not shown). Note that the above calculations are based on within-study differences in plasticity, an approach that has the benefits of standardizing protocols for a given plasticity comparison and controlling for variation among studies in average plasticity.

We categorized studies according to taxon (13 plants and 7 invertebrates), and data points according to trait types (life history, morphology or physiology). Life-history traits included those related to flowering and seed production in plants, and to egg production and egg size in invertebrates. Morphological traits in plants included overall biomass, biomass and growth rate of non-reproductive structures, plant height, and meristic traits such as the number of branches (Chun *et al.*, 2007) and leaves (DeWalt *et al.*, 2004). Morphological traits in invertebrates included overall body size and the size of physical structures, such as wing length and wing area in *Drosophila* (Gilchrist and Huey, 2004), beak length in soapberry bugs (Carroll *et al.*, 1997, 2005), and shell thickness in snails (Trussell and Smith, 2000). Physiological traits in plants included photosynthetic and chemical properties, and in invertebrates included the response to light in *Daphnia* (Cousyn *et al.*, 2001). Two studies (Carroll *et al.*, 1997, 1998) were considered as a single study for analysis (see below) because they examined the same populations and used the same common-garden treatments (although they examined different traits). The database used for analyses is available on request from the corresponding author (E.C.).

We used meta-analytic procedures to statistically evaluate the questions raised in the Introduction. Analyses were based on analyses of covariance (ANCOVAs; Type III sums of squares in SPSS v. 16.0) that used either darwin or haldane numerators as the dependent variable. All ANCOVAs included years (darwins) or generations (haldanes) as a covariate (as in Kinnison and Hendry, 2001; Hendry *et al.*, 2008; Dairmont *et al.*, 2009). This covariate provides a way to test and control for the possibility that greater evolutionary changes accrue with time, and it can also inform whether evolutionary change in plasticity is abrupt or gradual (Gingerich, 2001; Kinnison and Hendry, 2001; Sheets and Mitchell, 2001). All ANCOVAs included taxon and trait type as fixed factors, and also the taxon \times trait type interaction. The inclusion of these factors allows us to infer whether different taxa and types of traits show different patterns of plasticity evolution.

We performed four ANCOVAs, with two types of ANCOVAs for each type of evolutionary rate numerator (darwin and haldane). The first type of ANCOVA included all data points (i.e. all darwin or haldane numerators) and, in addition to the above factors, also included ‘study’ as a random factor (nested within taxon). The inclusion of this random factor controlled for variation among studies within a taxon or trait type. The second type of ANCOVA included the mean evolutionary rate numerator for each trait within a study (i.e. when a study examined the same trait in multiple sets of populations). ‘Study’ was not included as a random factor in the second type of ANCOVA because its inclusion did not allow for sufficient degrees of freedom when testing the main effects. The rationale for using two different types of ANCOVAs is that the first reduces pseudo-replication associated with multiple measures within a single study and the second reduces pseudoreplication associated with multiple data points for a single trait within a study (both reductions could not be simultaneously accomplished). In summary, the first (1) and second (2) types of ANCOVAs had the following structure:

- (1) evolutionary rate numerator \sim taxon + trait type + study(taxon) + time + taxon*trait type
- (2) mean evolutionary rate numerator \sim taxon + trait type + time + taxon*trait type

where a plus symbol separates effects, an asterisk represents an interaction, and parentheses indicate nesting. In all ANCOVAs, data points were weighted (i.e. weighted least-squares ANCOVAs) according to the average sample size used to collect those data points, so that studies with larger sample sizes were given greater weight. Additional weighting by variability (Arnqvist and Wooster, 1995; Gurevitch and Hedges, 1999) could not be performed because the necessary data were not available for some of the studies.

The four ANCOVAs each provided *P*-values for taxon, trait type, the taxon \times trait type interaction, and the time covariate. To obtain overall significance levels for a given term across the four ANCOVAs, we used the binomial likelihood function [following the equations in Chapman *et al.* (1999)]. Using this approach, any factor, covariate or interaction that was significant in two or more of the four tests is also significant overall at an α of 0.05. To determine whether darwin or haldane numerators differed from zero for specific combinations of taxon and trait type, we examined 95% confidence intervals obtained from the ANCOVAs. Again, values were considered to be significantly different from zero if 95% confidence intervals did not contain zero in two or more of the four tests.

All of the above analyses were repeated using absolute (unsigned) values. The *actual* (signed) values indicate the direction of plasticity evolution, whereas the *absolute* values indicate the overall magnitude of plasticity evolution, regardless of its direction. Thus, the analyses of absolute values can inform whether greater magnitudes of plasticity evolution occur for some taxa and trait types, but does not tell us whether this evolution is with respect to increased or decreased levels of plasticity. These analyses can also inform whether the amount of evolutionary change in plasticity changes through time. Given that many of our questions focus on *directions* of evolutionary change, we focus our discussion on analyses based on the actual values.

RESULTS

Most of the evolutionary rates differed from zero, indicating evolutionary change in plasticity following anthropogenic disturbance, in which increases in plasticity were more common than decreases (Table 1; Figs. 1 and 2). With respect to *directional* evolutionary change in plasticity, we found no main effects of taxon, some main effects of trait type, and

Table 1. The number (and percentage) of darwin numerators that were positive (increases in plasticity), negative (decreases in plasticity) or zero (no difference in plasticity between disturbed and undisturbed populations) for each taxon and trait type

	Positive	Negative	No change
Total	231 (61%)	136 (36%)	14 (4%)
Plants	123 (58%)	77 (36%)	12 (6%)
Invertebrates	108 (64%)	59 (35%)	2 (1%)
Life history	35 (49%)	32 (44%)	5 (7%)
Morphology	58 (55%)	38 (36%)	9 (9%)
Physiology	138 (68%)	66 (32%)	0 (0%)

Note: The results are presented for darwin numerators only because the direction of darwin and haldane numerators was always identical, but haldane numerators could not be calculated for all measures.

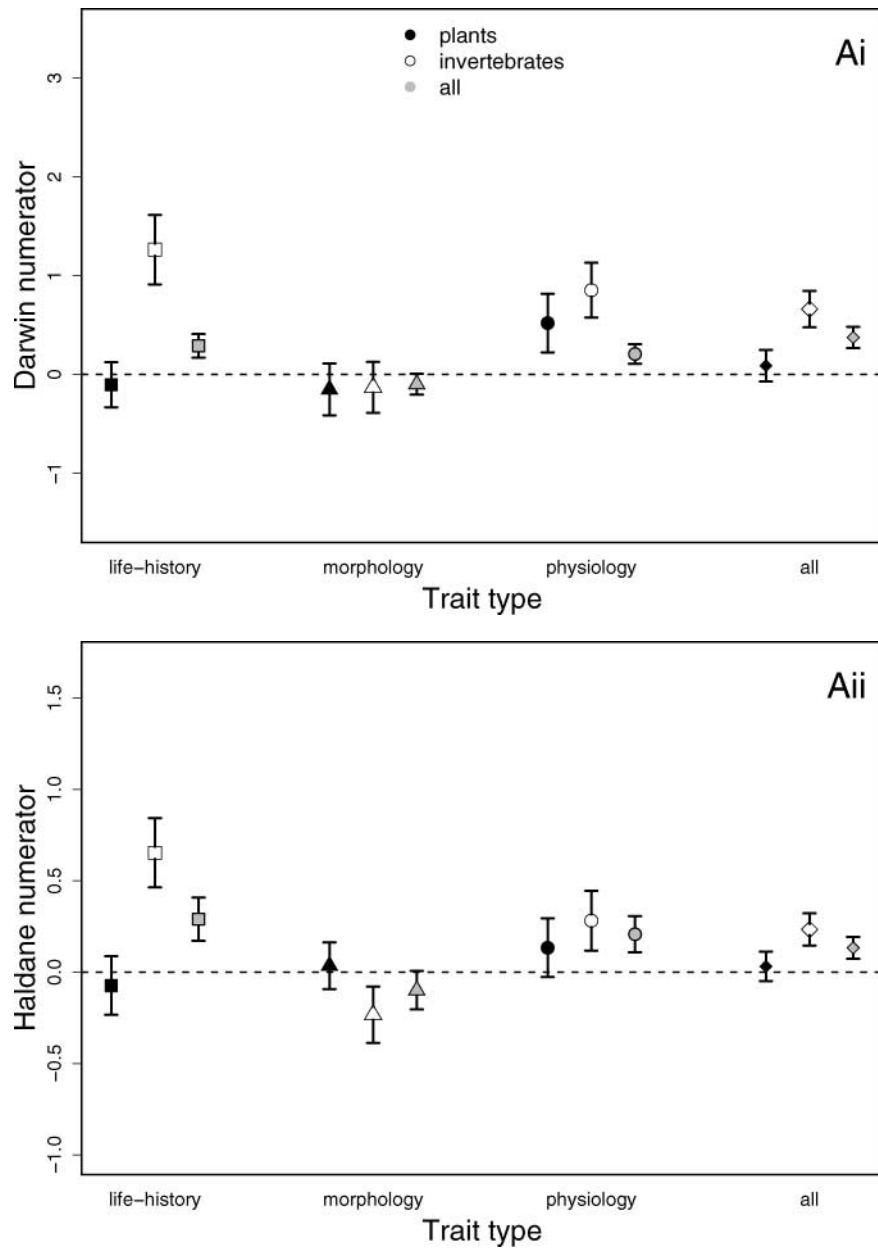
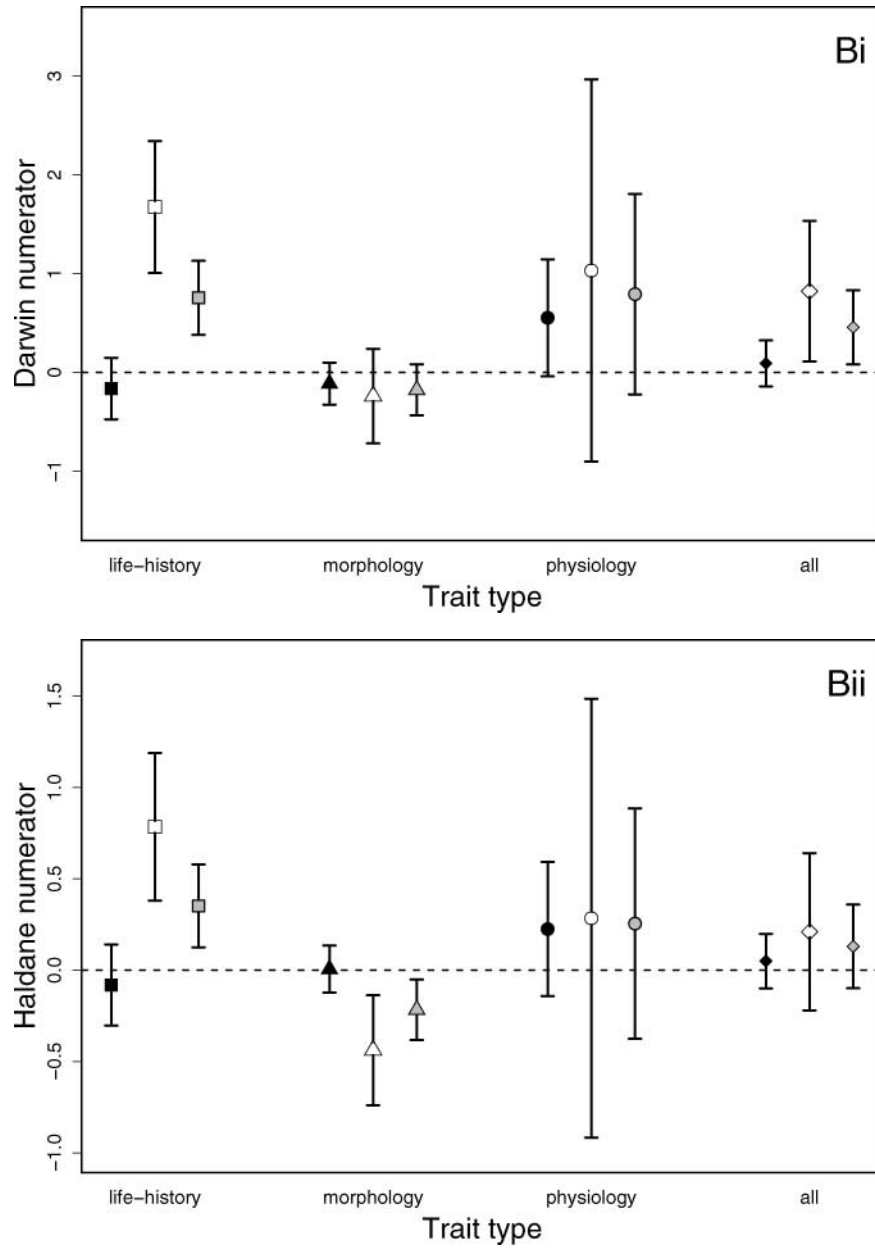


Fig. 1. Magnitude (actual values) of phenotypic change (i.e. evolutionary rate numerators) for plasticity for three trait types (life-history, morphology, and physiology) and for two taxa (plants and invertebrates) individually and combined. Values are the marginal means (\pm 95% confidence intervals) extracted from weighted least-squares ANCOVAs including trait type, taxon, their interaction, and



time since disturbance. (A) All data points within a study, (B) mean value for each trait within a study; (i) darwin numerators, (ii) haldane numerators. Solid points, plants; open points, invertebrates; grey points, the two combined.

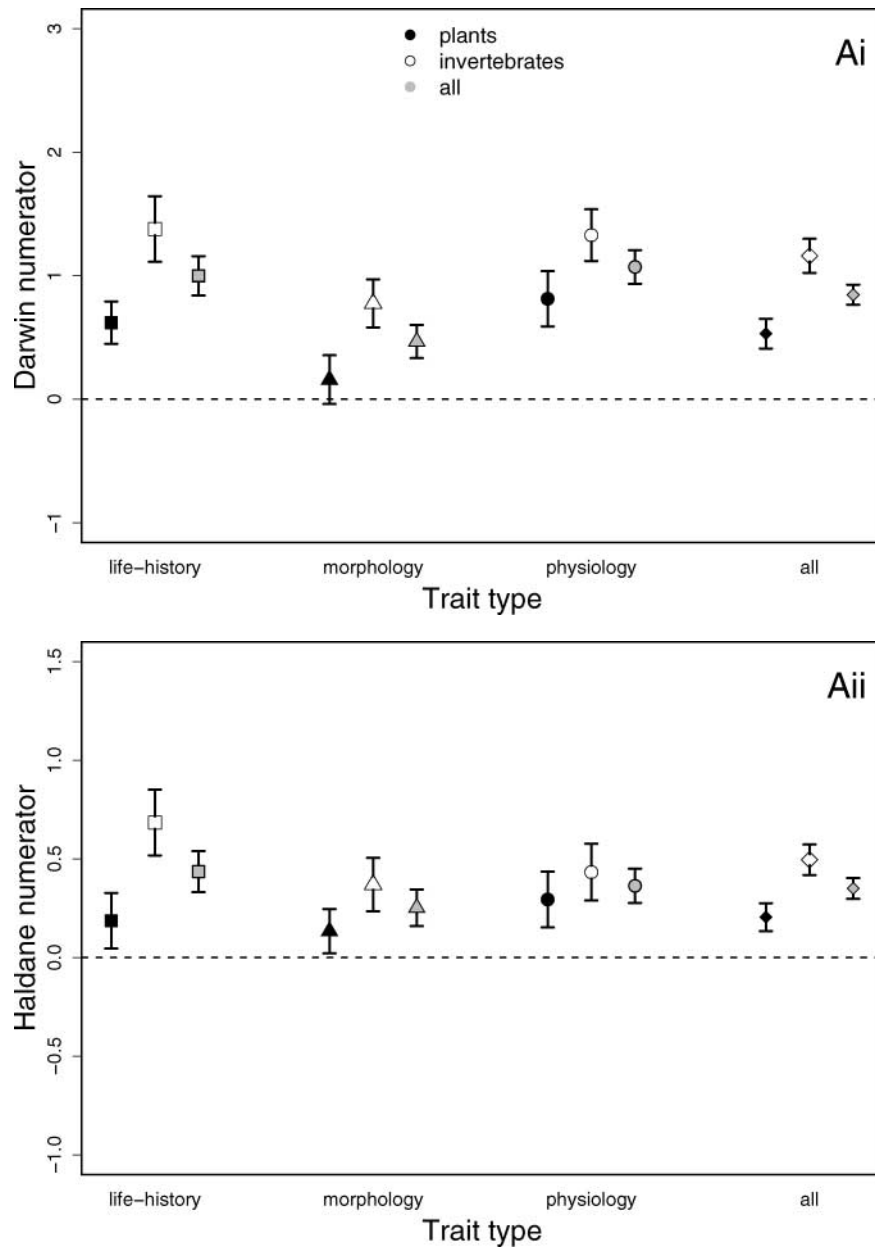
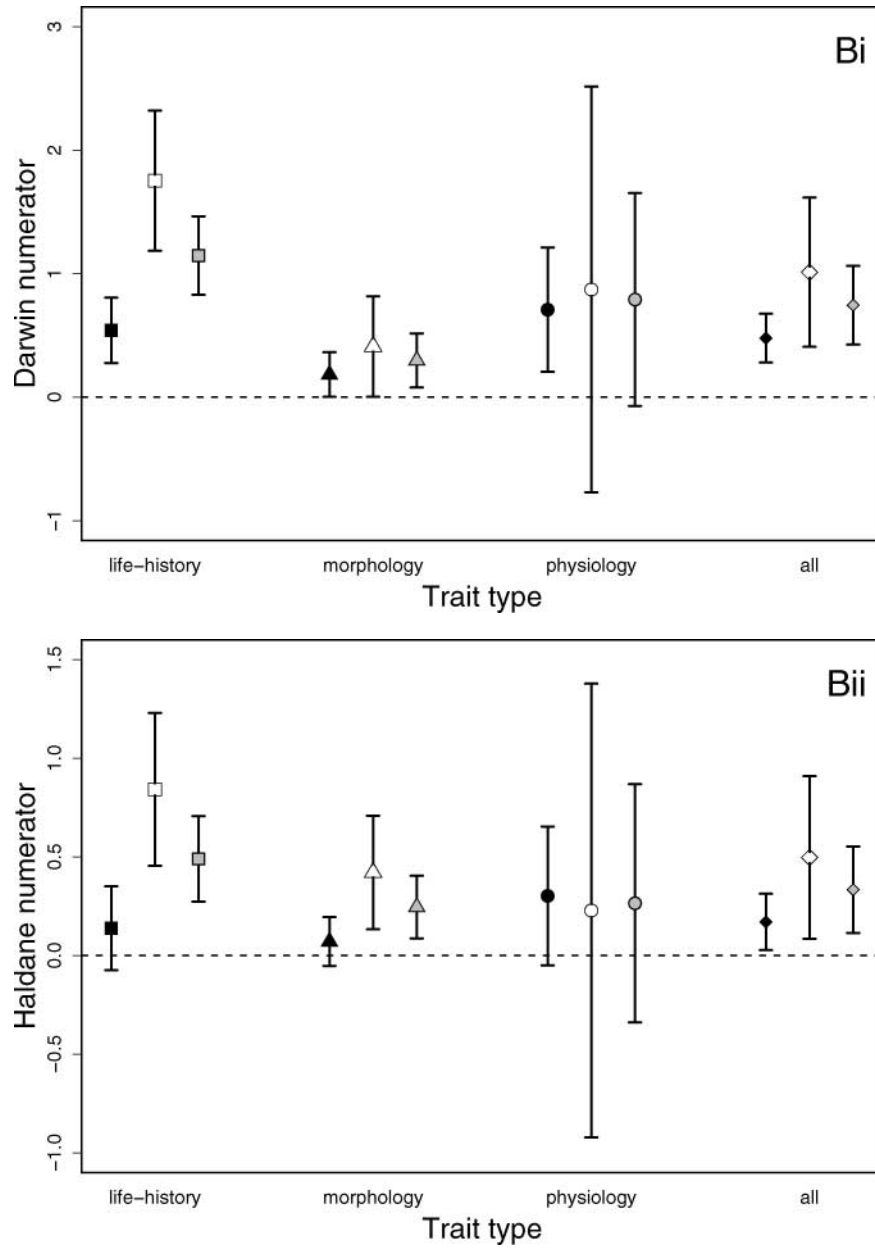


Fig. 2. Magnitude (absolute values) of evolutionary rate numerators for plasticity for three trait types (life-history, morphology, and physiology) and for two taxa (plants and invertebrates) individually and combined. Values are the marginal means (\pm 95% confidence intervals) extracted from weighted least-squares ANCOVAs including trait type, taxon, their interaction, and time since disturbance.



(A) All data points within a study, (B) mean value for each trait within a study; (i) absolute darwin numerators, (ii) absolute haldane numerators. Solid points, plants; open points, invertebrates; grey points, the two combined.

Table 2. Results from weighted least-squares ANCOVAs comparing evolutionary change in plasticity (darwin or haldane numerator) between taxa and among trait types

	Darwins			Haldanes		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
All data points						
Taxon	1	0.058	0.810	1	0.634	0.427
Trait type	2	2.502	0.083	2	3.378	0.035
Taxon*trait type	1	12.537	<0.001	1	18.338	<0.001
Study	16	1.702	0.044	13	3.967	<0.001
Time	1	0.045	0.831	1	0.087	0.768
Trait means						
Taxon	1	3.842	0.055	1	0.504	0.481
Trait type	2	9.140	<0.001	2	8.302	0.001
Taxon*trait type	2	9.867	<0.001	2	10.851	<0.001
Time	1	6.330	0.015	1	0.705	0.405
Error	60			53		

Note: The analysis also includes time (years or generations) to test for an effect of time since the anthropogenic disturbance on phenotypic change. Studies were weighted according to the average sample size.

interactions between taxon and trait type (Table 2). These interactions indicate that the effect of trait type on the evolution of plasticity differs between plants and invertebrates. For invertebrates, evolutionary rate numerators were, on average, (1) positive (i.e. increased plasticity after disturbance) for life-history traits in all four ANCOVAs, (2) positive for the single physiological trait in two ANCOVAs (non-significant in the other two), (3) negative (i.e. decreased plasticity after disturbance) for morphological traits in two ANCOVAs (non-significant in the other two), and (4) positive for all traits combined in three ANCOVAs (non-significant in one) (Fig. 1). For plants, no overall trend towards increased or decreased plasticity was observed for any trait type or for all traits combined (Fig. 1). Considering invertebrates and plants together, rate numerators were (1) positive for life-history traits in all four ANCOVAs, (2) positive for physiological traits in two ANCOVAs (non-significant in the other two), (3) negative for morphological traits in one ANCOVA (non-significant in the other three), and (4) positive for all traits combined in three ANCOVAs (non-significant in one) (Fig. 1).

With respect to *overall* evolutionary change in plasticity (i.e. ignoring the direction of plasticity evolution), we found effects of trait type and the interaction between taxon and trait type in one test only, and they were thus considered non-significant overall (Table 3; Fig. 2). The effects of taxon were not significant in any test. The reduced significance in the tests using the absolute values relative to the tests using the actual values reveals that trends in plasticity evolution among taxa and trait types are with respect to *directional* change in plasticity, rather than overall magnitudes of plasticity evolution.

Time since disturbance was significant in only one of four ANCOVAs (Table 2) and was thus considered non-significant overall (as above). This result suggests that evolutionary change in plasticity remains similar across different time intervals – that is, any evolutionary

Table 3. Results from weighted least-squares ANCOVAs comparing evolutionary change in plasticity (*absolute value* of darwin or haldane numerator) between taxa and among trait types

	Darwins			Haldanes		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
All data points						
Taxon	1	1.641	0.201	1	0.047	0.829
Trait type	2	0.187	0.829	2	1.781	0.170
Taxon*trait type	1	2.030	0.155	1	1.200	0.274
Study	16	1.422	0.128	13	6.078	<0.001
Time	1	1.694	0.194	1	0.007	0.933
Trait means						
Taxon	1	2.846	0.097	1	2.280	0.137
Trait type	2	9.809	<0.001	2	1.669	0.198
Taxon*trait type	2	3.539	0.035	2	1.218	0.304
Time	1	2.140	0.149	1	0.057	0.813
Error	60			53		

Note: The analysis also includes time (years or generations) to test for an effect of time since the anthropogenic disturbance on phenotypic change. Studies were weighted according to the average sample size. **Bold** values were significant in the test using *actual* signed values, but not in the test using *absolute* unsigned values.

change in plasticity occurs rapidly with little subsequent change (Fig. 3). This result also held when considering the absolute values of evolutionary rate numerators (Table 3). The nested effect of study was significant in the tests using actual (signed) values (Table 2), indicating that plasticity evolution differed among studies *within* a given taxon and trait type.

DISCUSSION

The above results suggest no common trend across taxa and trait types for the evolution of plasticity following anthropogenic disturbance. They instead reveal idiosyncrasies related to specific trait types within specific taxa. To highlight one example, invertebrates often evolved increased plasticity for life-history traits (and for the single physiological trait) but evolved decreased plasticity for morphological traits. These differences might be due to how *rapidly* and/or *strongly* different trait types respond plastically to environmental disturbance (see Introduction). For example, many morphological traits respond plastically only during development (e.g. Aubret *et al.*, 2004; Grünbaum *et al.*, 2007; Hoverman and Relyea, 2007), whereas at least some life-history (e.g. Fischer *et al.*, 2003; Dzikowski *et al.*, 2004) and physiological (e.g. Timmerman and Chapman, 2004; Seebacher, 2005) traits can continue to respond plastically throughout life. The adaptive value of (and selection on) plasticity for the latter types of traits might therefore be higher, at least within invertebrates. In contrast, we did not detect any general trend (increase or decrease) in the evolution of plasticity in plants – plasticity increased for some traits but decreased for others, even within a trait type.

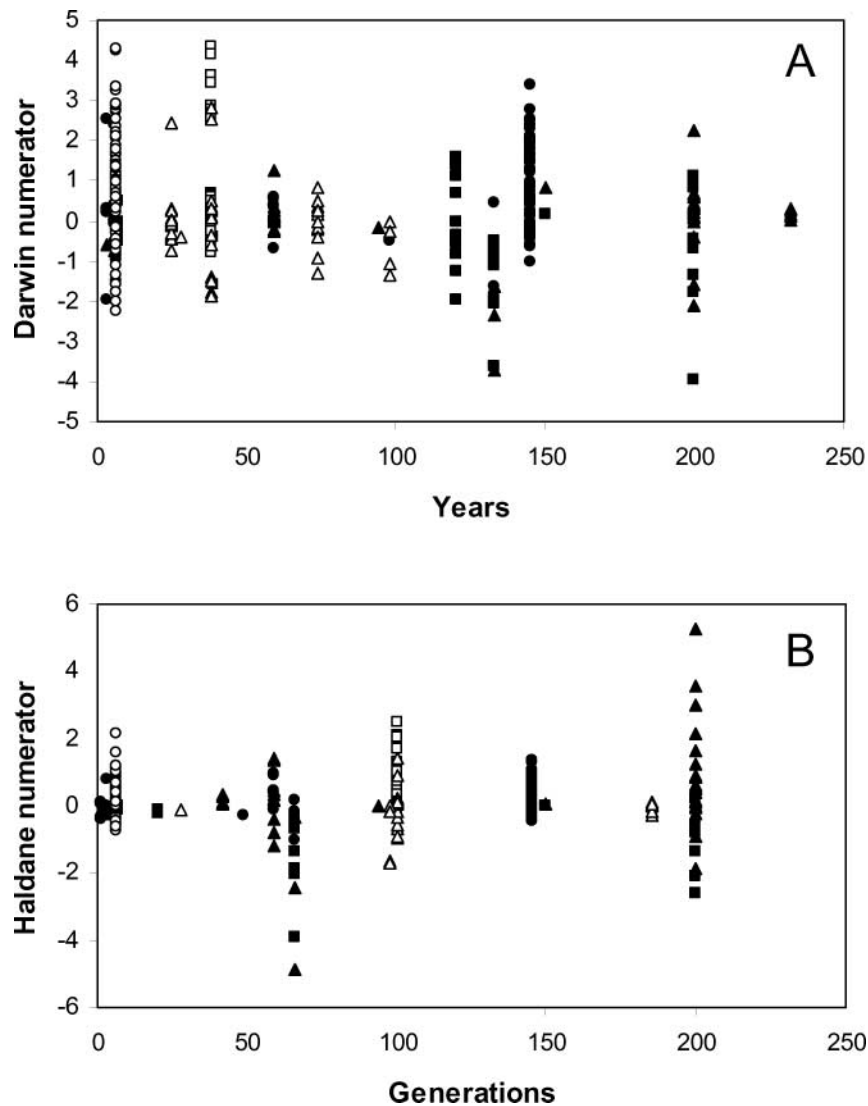


Fig. 3. Magnitude of phenotypic change (i.e. evolutionary rate numerators) as a function of time (years or generations) since the anthropogenic disturbance. (A) Darwin numerator, (B) haldane numerator. Solid points, plants; open points, invertebrates. Squares, life-history traits; triangles, morphological traits; circles, physiological traits. All data points from each study are presented.

Increased levels of plasticity often occurred in disturbed populations. An example for invertebrates comes from soapberry bugs (*Jadera haematoloma*). Here, plasticity in egg number was evident in bugs from the *introduced host plant* in nature when raised on introduced versus native host plants (more eggs on the introduced host plant), even though significant plasticity between these rearing environments was *not* evident in bugs from the *native host plant* (Carroll *et al.*, 1998). Another example comes from *Daphnia magna*. Here, increased plasticity in vertical migrations was evident in *Daphnia* in response to fish

pheromones in a population collected after the introduction of fish predators in nature – plasticity was lower in the same population before the introduction (Cousyn *et al.*, 2001; Hairston and De Meester, 2008). For plants, introduced populations of *Sapinum sebiferum* trees showed increased plasticity, relative to trees in their native range, in biomass and leaf area in response to different light conditions (Zou *et al.*, 2009). Similarly, invasive purple loosestrife (*Lythrum salicaria*) showed increased plasticity, relative to non-invasive purple loosestrife, in above-ground biomass in response to different water and nutrient conditions (Chun *et al.*, 2007). In these examples, the plastic response is in the same *direction* between disturbed and undisturbed populations, suggesting that the evolution of increased plasticity might be important for adaptation following anthropogenic disturbance.

In other cases, *decreased* levels of plasticity occurred in disturbed populations. An example for plants comes from *Plantago major*. Here, plasticity in growth rate in response to ozone (reduced growth in the presence of ozone) was lower in seeds collected *after* increases in atmospheric ozone concentration (Davison and Reiling, 1995). An example for invertebrates comes from *Daphnia galeata*. Here, plasticity in growth rate in response to food quality (reduced growth on lower-quality food) was lower for populations collected *after* anthropogenic induction of low-quality food sources (Hairston *et al.*, 2001; Hairston and De Meester, 2008). Another example comes from snails (*Littorina obtusata*). Here, decreased plasticity in shell thickness was evident in *L. obtusata* in response to crab predators in the population collected from an area with introduced crab predators in nature, relative to those from an area *without* introduced crab predators (Trussell and Smith, 2000).

We can envision two likely explanations for the evolution of reduced plasticity described above. In the first case, the plastic response might simply be a maladaptive consequence of reduced resource acquisition under novel environmental conditions (i.e. conditions under which the populations have not evolved), sometimes called ‘passive’ plasticity (van Kleunen and Fischer, 2005). Examples include the aforementioned reduced growth of *Plantago major* and *Daphnia galeata* after anthropogenic disturbance – maladaptive plasticity in growth becomes reduced in populations adapting to low-quality conditions. In the second case, the direction of plasticity might be adaptive but its expression is more costly in the new environment, such that the fitness costs now outweigh the benefits of plasticity (DeWitt, 1998; DeWitt *et al.*, 1998; Weinig and Delph, 2001; Langerhans and DeWitt, 2002; Relyea, 2002; Relyea and Auld, 2005). An example might include the aforementioned response of snails to crab predators – decreased plasticity in shell thickness could have resulted from associated costs in the form of reduced growth, coupled with the evolution of increased shell thickness, which would make plasticity less important for adaptation (Trussell and Smith, 2000).

We also observed some instances in which plasticity did not evolve. Possible reasons for a lack of plasticity evolution in nature could include no genetic variation for plasticity (e.g. Brommer *et al.*, 2005; Charmantier *et al.*, 2008), no selection on plasticity (i.e. no difference in fitness between plastic and non-plastic individuals), adaptation via the evolution of genetic components of *other* traits (i.e. other than the focal trait), and migration that homogenizes populations (Edelaar *et al.*, 2005; Crispo, 2008).

We found no evidence that the amount of evolutionary change in plasticity changes with time. Other recent meta-analyses on natural populations have also found no influence of time on the amount of evolutionary change (Estes and Arnold, 2007; Hendry *et al.*, 2008; Dairmont *et al.*, 2009). A possible biological reason for this result includes strong selective sweeps that rapidly deplete genetic variation (i.e. rapid evolution of plasticity). Of course, no relationship between evolutionary change and time would be observed when there is no evolution of

plasticity (i.e. no genetic variation for plasticity or no selection on plasticity). A possible methodological reason for this result is that our analyses examine different points in time *across* studies, rather than examining temporal trends *within* studies. Indeed, analyses of phenotypic change within lineages do tend to reveal greater phenotypic change with greater lengths of time (Schluter, 2000; Kinnison and Hendry, 2001).

CAVEATS, CONCLUSIONS, AND IMPLICATIONS

Our analyses were limited in several respects. First, our database included only the small number of studies for which evolutionary rates could be calculated for plasticity in response to anthropogenic disturbance. This led to data for only a few types of anthropogenic disturbances, species, traits, and common-garden treatments. Second, different types of anthropogenic disturbance might cause different types of plasticity evolution but our database was too small to evaluate this possibility. Third, the specific common-garden treatments used in individual studies might have led to patterns of plasticity that differed from those that occur in nature (i.e. if the treatments did not closely mimic natural conditions). Fourth, pseudoreplication could be apparent when multiple traits were sampled within a trait type within studies, and if traits are functionally integrated such that covariation in plastic responses occurs [i.e. ‘plasticity integration’ (Parsons and Robinson, 2006)]. Fifth, the changes in plasticity documented in our database might not be *biologically* significant, even if they are *statistically* significant (e.g. they could be due to drift). Clearly, additional data would greatly aid inferences from studies such as ours, and about plasticity evolution in general.

Despite these limitations, we are still able to note a few important observations that are likely robust. First, plasticity often evolves in response to environmental disturbance. Second, evolutionary changes in plasticity are expected to differ among types of traits and taxa. Third, the magnitude of change in plasticity is generally unrelated to time since anthropogenic disturbance, suggesting that evolutionary changes in plasticity are abrupt. The evolution of plasticity might permit adaptive responses to changing conditions (for reviews, see Alpert and Simms, 2002; Price *et al.*, 2003; Badyaev, 2005; Crispo, 2007; Ghalambor *et al.*, 2007; Carroll, 2008; Gienapp *et al.*, 2008; Hairston and De Meester, 2008; Visser, 2008). Little is known about the *evolution* of plasticity as an adaptive response, but this evolution could be important for population persistence in a variety of natural systems. Future study should focus on the contributions (positive or negative) of plasticity to population persistence. In particular, additional research on the genetic basis and heritability of plasticity is needed so that we can gain a better understanding of conditions under which plasticity is expected to evolve.

ACKNOWLEDGEMENTS

We thank the individuals who provided additional information not presented in the manuscripts used in the database: Luc De Meester, Saara DeWalt, George Gilchrist, Nelson Hairston, Jr., Sylvan Kaufman, Kristin Lewis, Gretchen Meyer, Kirk Moloney, and Lorne Wolfe. The development of this study was facilitated through discussions with Maryse Boisjoly, Tariq Gardezi, Renaud Kaeuffer, and Jean-Sébastien Moore. Thomas Farrugia and Michael Kinnison assisted with building the database. Funding was provided by the Natural Sciences and Engineering Research Council of Canada (E.C., J.D.D., X.T.-P., A.E.M., and A.P.H.), the Comisión Nacional de Investigación Científica y Tecnológica of the Government of Chile (C.C.), Le Fonds Québécois de la Recherche sur la Nature et

les Technologies (A.K.S.), the Roche Research and the Stiefel-Zangger Foundation (D.B.), and Secretaría Nacional de Ciencia y Tecnología de Panama (L.F.D.).

REFERENCES

- Ahern, R.G., Hawthorne, D.J. and Raupp, M.J. 2009. Founder effects and phenotypic variation in *Adelges cooleyi*, an insect pest introduced to the eastern United States. *Biol. Invasions*, **11**: 959–971.
- Alpert, P. and Simms, E.L. 2002. The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evol. Ecol.*, **16**: 285–297.
- Antonovics, J. and Bradshaw, A.D. 1970. Evolution in closely adjacent plant populations 8. Clinal patterns at a mine boundary. *Heredity*, **25**: 349–362.
- Arnqvist, G. and Wooster, D. 1995. Meta-analysis: synthesizing research findings in ecology and evolution. *Trends Ecol. Evol.*, **10**: 236–240.
- Aubret, F., Shine, R. and Bonnet, X. 2004. Adaptive developmental plasticity in snakes. *Nature*, **431**: 261–262.
- Badyaev, A.V. 2005. Stress-induced variation in evolution: from behavioural plasticity to genetic assimilation. *Proc. R. Soc. Lond. B*, **272**: 877–886.
- Brommer, J.E., Merilä, J., Sheldon, B.C. and Gustafsson, L. 2005. Natural selection and genetic variation for reproductive reaction norms in a wild bird population. *Evolution*, **59**: 1362–1371.
- Bumpus, H. 1899. The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. *Mar. Biol. Lab., Biol. Lect., Woods Hole*, 209–228.
- Bürger, R. and Lynch, M. 1995. Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution*, **49**: 151–163.
- Cain, A.J. and Sheppard, P.M. 1954. Natural selection in *Cepaea*. *Genetics*, **39**: 89–116.
- Carroll, S.P. 2008. Facing change: forms and foundations of contemporary adaptation to biotic invasions. *Mol. Ecol.*, **17**: 361–372.
- Carroll, S.P., Dingle, H. and Klassen, S.P. 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. *Evolution*, **51**: 1182–1188.
- Carroll, S.P., Klassen, S.T.P. and Dingle, H. 1998. Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. *Evol. Ecol.*, **12**: 955–968.
- Carroll, S.P., Loye, J.E., Dingle, H., Mathieson, M., Famula, T.R. and Zalucki, M.P. 2005. And the beak shall inherit – evolution in response to invasion. *Ecol. Lett.*, **8**: 944–951.
- Caruso, C.M., Maherali, H. and Sherrard, M. 2006. Plasticity of physiology in *Lobelia*: testing for adaptation and constraint. *Evolution*, **60**: 980–990.
- Chapman, R.W., Sedberry, G.R., Koenig, C.C. and Eleby, B.M. 1999. Stock identification of gag, *Mycteroperca microlepis*, along the southeast coast of the United States. *Mar. Biotech.*, **1**: 137–146.
- Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. and Sheldon, B.C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, **320**: 800–803.
- Chun, Y.J., Collyer, M.L., Moloney, K.A. and Nason, J.D. 2007. Phenotypic plasticity of native vs. invasive purple loosestrife: a two-state multivariate approach. *Ecology*, **88**: 1499–1512.
- Clobert, J., Le Galliard, J.F., Cote, J., Meylan, S. and Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.*, **12**: 197–209.
- Cousyn, C., De Meester, L., Colbourne, J.K., Brendonck, L., Verschuren, D. and Volckaert, F. 2001. Rapid, local adaptation of zooplankton behavior to changes in predation pressure in the absence of neutral genetic changes. *Proc. Natl. Acad. Sci. USA*, **98**: 6256–6260.
- Crispo, E. 2007. The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution*, **61**: 2469–2479.

- Crispo, E. 2008. Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. *J. Evol. Biol.*, **21**: 1460–1469.
- Dairmont, C.T., Carlson, S.M., Kinnison, M.T. and Paquet, P.C. 2009. Human predators outpace other agents of trait change in the wild. *Proc. Natl. Acad. Sci. USA*, **106**: 952–954.
- Danielson-François, A.M., Kelly, J.K. and Greenfield, M.D. 2006. Genotype \times environment interaction for male attractiveness in an acoustic moth: evidence for plasticity and canalization. *J. Evol. Biol.*, **19**: 532–542.
- Davison, A.W. and Reiling, K. 1995. A rapid change in ozone resistance of *Plantago major* after summers with high ozone concentrations. *New Phytol.*, **131**: 337–344.
- DeWalt, S.J., Denslow, J.S. and Hamrick, J.L. 2004. Biomass allocation, growth, and photosynthesis of genotypes from native and introduced ranges of the tropical shrub *Clidemia hirta*. *Oecologia*, **138**: 521–531.
- DeWitt, T.J. 1998. Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *J. Evol. Biol.*, **11**: 465–480.
- DeWitt, T.J., Sih, A. and Wilson, D.S. 1998. Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.*, **13**: 77–81.
- Donohue, K., Messiqua, D., Pyle, E.H., Heschel, M.S. and Schmitt, J. 2000. Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade-avoidance responses in *Impatiens capensis*. *Evolution*, **54**: 1956–1968.
- Dzikowski, R., Hulata, G., Harpaz, S. and Karplus, I. 2004. Inducible reproductive plasticity of the guppy *Poecilia reticulata* in response to predation cues. *J. Exp. Zool. A*, **301A**: 776–782.
- Edelaar, P., Piersma, T. and Postma, E. 2005. Retained non-adaptive plasticity: gene flow or small inherent costs of plasticity? *Evol. Ecol. Res.*, **7**: 489–495.
- Edelaar, P., Siepielski, A.M. and Clobert, J. 2008. Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution*, **62**: 2462–2472.
- Estes, S. and Arnold, S.J. 2007. Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales. *Am. Nat.*, **169**: 227–244.
- Etges, W.J., de Oliveira, C.C., Gragg, E., Ortíz-Barrientos, D., Noor, M.A.F. and Ritchie, M.G. 2007. Genetics of incipient speciation in *Drosophila mojavensis*. I. Male courtship song, mating success, and genotype \times environment interactions. *Evolution*, **61**: 1106–1119.
- Fischer, K., Brakefield, P.M. and Zwaan, B.J. 2003. Plasticity in butterfly egg size: why larger offspring at lower temperatures? *Ecology*, **84**: 3138–3147.
- Gabriel, W. 2006. Selective advantage of irreversible and reversible phenotypic plasticity. *Archiv Hydrobiol.*, **167**: 1–20.
- Gabriel, W., Luttbegg, B., Sih, A. and Tollrian, R. 2005. Environmental tolerance, heterogeneity, and the evolution of reversible plastic responses. *Am. Nat.*, **166**: 339–353.
- Ghalambor, C.K., McKay, J.K., Carroll, S.P. and Reznick, D.N. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.*, **21**: 394–407.
- Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A. and Merilä, J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.*, **17**: 167–178.
- Gilchrist, G.W. and Huey, R.B. 2004. Plastic and genetic variation in wing loading as a function of temperature within and among parallel clines in *Drosophila subobscura*. *Integr. Comp. Biol.*, **44**: 461–470.
- Gingerich, P.D. 2001. Rates of evolution on the time scale of the evolutionary process. *Genetica*, **112**: 127–144.
- Gomulkiewicz, R. and Holt, R.D. 1995. When does evolution by natural selection prevent extinction? *Evolution*, **49**: 201–207.
- Grünbaum, T., Cloutier, R., Mabee, P.M. and Le François, N.R. 2007. Early developmental plasticity and integrative responses in arctic charr (*Salvelinus alpinus*): effects of water velocity on body size and shape. *J. Exp. Zool. B*, **308B**: 396–408.

- Gurevitch, J. and Hedges, L.V. 1999. Statistical issues in ecological meta-analyses. *Ecology*, **80**: 1142–1149.
- Hairston, N.G. and De Meester, L. 2008. *Daphnia* paleogenetics and environmental change: deconstructing the evolution of plasticity. *Int. Rev. Hydrobiol.*, **93**: 578–592.
- Hairston, N.G., Holtmeier, C.L., Lampert, W., Weider, L.J., Post, D.M., Fischer, J.M. *et al.* 2001. Natural selection for grazer resistance to toxic cyanobacteria: evolution of phenotypic plasticity? *Evolution*, **55**: 2203–2214.
- Hendry, A.P. and Kinnison, M.T. 1999. The pace of modern life: measuring rates of contemporary microevolution. *Evolution*, **53**: 1637–1653.
- Hendry, A.P., Farrugia, T.J. and Kinnison, M.T. 2008. Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.*, **17**: 20–29.
- Houle, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics*, **130**: 195–204.
- Hoverman, J.T. and Relyea, R.A. 2007. How flexible is phenotypic plasticity? Developmental windows for trait induction and reversal. *Ecology*, **88**: 693–705.
- Hutchings, J.A., Swain, D.P., Rowe, S., Eddington, J.D., Puvanendran, V. and Brown, J.A. 2007. Genetic variation in life-history reaction norms in a marine fish. *Proc. R. Soc. Lond. B*, **274**: 1693–1699.
- Jacquemyn, H., Brys, R., Adriaens, D., Honnay, O. and Roldán-Ruiz, I. 2009. Effects of population size and forest management on genetic diversity and structure of the tuberous orchid *Orchis mascula*. *Conserv. Genet.*, **10**: 161–168.
- Kettlewell, H.B.D. 1958. A survey of the frequencies of *Biston betularia* (L.) (Lep.) and its melanic forms in Great Britain. *Heredity*, **12**: 51–72.
- Kinnison, M.T. and Hendry, A.P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica*, **112**: 145–164.
- Langerhans, R.B. and DeWitt, T.J. 2002. Plasticity constrained: over-generalized induction cues cause maladaptive phenotypes. *Evol. Ecol. Res.*, **4**: 857–870.
- Macnair, M.R. 1991. Why the evolution of resistance to anthropogenic toxins normally involves major gene changes: the limits to natural selection. *Genetica*, **84**: 213–219.
- Masel, J., King, O.D. and Maughan, H. 2007. The loss of adaptive plasticity during long periods of environmental stasis. *Am. Nat.*, **169**: 38–46.
- Maynard Smith, J. 1989. The causes of extinction. *Phil. Trans. R. Soc. Lond. B*, **325**: 241–252.
- Mousseau, T.A. and Roff, D.A. 1987. Natural selection and the heritability of fitness components. *Heredity*, **59**: 181–197.
- Nussey, D.H., Wilson, A.J. and Brommer, J.E. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.*, **20**: 831–844.
- Orr, H.A. and Unckless, R.L. 2008. Population extinction and the genetics of adaptation. *Am. Nat.*, **172**: 160–169.
- Padilla, D.K. and Adolph, S.C. 1996. Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol. Ecol.*, **10**: 105–117.
- Parsons, K.J. and Robinson, B.W. 2006. Replicated evolution of integrated plastic responses during early adaptive divergence. *Evolution*, **60**: 801–813.
- Petrin, Z., Englund, G. and Malmqvist, B. 2008. Contrasting effects of anthropogenic and natural acidity in streams: a meta-analysis. *Proc. R. Soc. Lond. B*, **275**: 1143–1148.
- Price, T.D., Qvarnström, A. and Irwin, D.E. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B*, **270**: 1433–1440.
- Relyea, R.A. 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology*, **82**: 523–540.
- Relyea, R.A. 2002. Costs of phenotypic plasticity. *Am. Nat.*, **159**: 272–282.
- Relyea, R.A. and Auld, J.R. 2005. Predator- and competitor-induced plasticity: how changes in foraging morphology affect phenotypic trade-offs. *Ecology*, **86**: 1723–1729.

- Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.*, **24**: 35–68.
- Schluter, D. 2000. *The Ecology of Adaptive Radiation*. New York: Oxford University Press.
- Schwartz, T.S. and Karl, S.A. 2005. Population and conservation genetics of the gopher tortoise (*Gopherus polyphemus*). *Conserv. Genet.*, **6**: 917–928.
- Seebacher, F. 2005. A review of thermoregulation and physiological performance in reptiles: what is the role of phenotypic flexibility? *J. Comp. Physiol. B*, **175**: 453–461.
- Sheets, H.D. and Mitchell, C.E. 2001. Uncorrelated change produces the apparent dependence of evolutionary rate on interval. *Paleobiology*, **27**: 429–445.
- Steinger, T., Roy, B.A. and Stanton, M.L. 2003. Evolution in stressful environments II: adaptive value and costs of plasticity in response to low light in *Sinapis arvensis*. *J. Evol. Biol.*, **16**: 313–323.
- Stirling, D.G., Reale, D. and Roff, D.A. 2002. Selection, structure and the heritability of behaviour. *J. Evol. Biol.*, **15**: 277–289.
- Stomp, M., van Dijk, M.A., van Overzee, H.M.J., Wortel, M.T., Sigon, C.A.M., Egas, M.H. *et al.* 2008. The timescale of phenotypic plasticity and its impact on competition in fluctuating environments. *Am. Nat.*, **172**: E169–E185.
- Sultan, S.E. and Spencer, H.G. 2002. Metapopulation structure favors plasticity over local adaptation. *Am. Nat.*, **160**: 271–283.
- Timmerman, C.M. and Chapman, L.J. 2004. Behavioral and physiological compensation for chronic hypoxia in the sailfin molly (*Poecilia latipinna*). *Physiol. Biochem. Zool.*, **77**: 601–610.
- Trussell, G.C. and Smith, L.D. 2000. Induced defenses in response to an invading crab predator: an explanation of historical and geographic phenotypic change. *Proc. Natl. Acad. Sci. USA*, **97**: 2123–2127.
- Van Buskirk, J. and Steiner, U.K. 2009. The fitness costs of developmental canalization and plasticity. *J. Evol. Biol.*, **22**: 852–860.
- van Kleunen, M. and Fischer, M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytol.*, **166**: 49–60.
- Via, S. and Lande, R. 1985. Genotype–environment interaction and the evolution of phenotypic plasticity. *Evolution*, **39**: 505–522.
- Via, S., Gomulkiewicz, R., de Jong, G., Scheiner, S.M., Schlichting, C.D. and Van Tienderen, P.H. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.*, **10**: 212–217.
- Visser, M.E. 2008. Keeping up with a warming world: assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B*, **275**: 649–659.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. and Melillo, J.M. 1997. Human domination of Earth's ecosystems. *Science*, **277**: 494–499.
- Weinig, C. and Delph, L.F. 2001. Phenotypic plasticity early in life constrains developmental responses later. *Evolution*, **55**: 930–936.
- Zou, J.W., Rogers, W.E. and Siemann, E. 2009. Plasticity of *Sapium sebiferum* seedling growth to light and water resources: inter- and intraspecific comparisons. *Basic Appl. Ecol.*, **10**: 79–88.