Supporting Information for:

Human influences on the strength of phenotypic selection

Vincent Fugère & Andrew Hendry Correspondence to: vincent.fugere@mail.mcgill.ca

This file includes:

Supplementary Methods & Results Tables S1 to S4 Figures S1 to S5 Data sources

Supplementary Methods & Results

Properties of studies included in the database

All data sources are referenced at the end of this document. We classified systems based on major taxa (vertebrate, invertebrate, or plant), type of disturbance, experimental design, and fitness component(s), to explore whether these moderator variables could influence human impacts on selection strength. Types of human disturbances included in the database were: (1) climate change, defined as an increase in ambient temperature and/or CO2 concentration (in controlled experiments, as noted in the main text); (2) habitat degradation/modification, including anthropogenic fire, pollution, eutrophication, land conversion, habitat fragmentation, and pollinator loss; (3) harvest, including fishing, hunting, and gathering of wild organisms; (4) invasion, whereby selection is measured in a native population experiencing the presence of a newly-introduced species; and (5) introduction, whereby selection is measured in a population that was moved by humans to a new location.

Types of experimental designs included: (1) temporal comparison of selection before and after disturbance within a single population; (2) spatial comparison of selection at any given time between disturbed and natural populations; (3) experimental simulation of the disturbance, e.g., warming chambers; (4) selection partitioning, whereby anthropogenic and natural selection can be distinguished within a single population, for example exploited fish stocks in which both natural and fishing mortality can be recorded. For two systems, we compared selection between two or more congeneric species (native vs. invasive, respectively corresponding to natural vs. disturbed conditions) for the same set of traits and in the same locality; we termed this design 'species comparison'. For experimental studies, we further split systems into three categories based on the expected level of maladaptation in control ('natural') conditions. We noted if selection in natural conditions was measured *in situ* in the field on a native population ('field, native'), *in situ* in the field on an exotic population relatively naive to local conditions ('field,

exotic'), or in a laboratory environment to which all populations are naive regardless of whether they are native or exotic ('laboratory'). One might expect stronger selection in control conditions in the latter two contexts if the population is maladapted to the control environment, which could then mask any effect of disturbance. Finally, we also classified systems based on the fitness components used to calculate selection, namely: (1) biomass, growth, or condition; (2) fecundity (e.g., number of eggs or seeds); (3) mating success; (4) survival; and (5) 'composite', when more than one fitness component was used to measure fitness.

We also classified all traits into four different categories, following previous studies that reported differences in selection strength among trait types (1, 2). Note that trait category is a property of individual selection coefficients, not of systems (as several systems included multiple traits). Trait categories included 'size' (a length or mass measurement of overall organism size, or a body part measurement used by the authors as a proxy for organism size), 'morphology' (morphological traits other than body size, e.g. coloration or the relative length of a given body part which does not obviously correlate with body size), 'life history' (e.g., migration date or growth rate), and 'physiology' (e.g., concentration of a given chemical compounds). The latter category also included the few behavioral traits in the database. Five traits did not fit any category (e.g., a feature of a superorganism's nest) and were thus excluded from analyses.

Table S1 reports the number of systems and selection coefficients available for each class of each moderator variable. Most studies included in the final database focused on plants or vertebrates rather than invertebrates, and most used experimental approaches or spatial comparisons to contrast selection in natural and disturbed conditions. Authors calculated relative fitness based on a variety of fitness components, with survival being the most common metric. Body size was by far the most common trait in the database, and selection coefficients for physiological/behavioral traits were very rare (Table S1).

Maximum selection strength

In addition to mean selection strength, we also modeled maximum selection strength using linear quantile mixed models (LQMMs) to estimate the 99th conditional quantile of |*S*| or $|\beta|$. Models were fitted with the R package 'lqmm' (3), using a Nelder-Mead optimization algorithm to find maximum likelihood parameter estimates. LQMMs included the same fixed effects as the LMMs of mean selection strength; however, the lqmm package does not allow for nested random effects. We therefore used 'system' as the only random intercept. To assess whether our results were affected by potential within-trait correlations, we fitted two LQMMs per coefficient type: one model used the full data set (ignoring non-independence among multiple estimates from the trait), and one model used a 'pooled' dataset where each trait has a single (mean) value in either disturbance conditions (thus eliminating within-trait correlations). Standard errors and statistical significance of model coefficients were determined using block bootstrapping (100 replications).

The results for maximum selection strength followed the same general pattern than the results for mean selection strength (i.e., an overall negative effect of disturbance on selection

strength except for some harvested systems showing strong positive effects of disturbance; Fig. S2). However, the effect of disturbance type or conditions were weaker and not statistically significant in QLMMs (Table S3).

Effect of disturbance on selection strength across various moderator variables

We explored how our results could be influenced by variation among studies in focal taxa, types of disturbance, study designs, and fitness components. The limited number of systems with standard errors available (18 for $|S|$ and 20 for $|\beta|$) precludes a formal meta-analysis of these potential influences. We instead used all data available and ignored observation-level uncertainty, calculating for each trait from each system an effect size of human disturbance. These effect sizes were log response ratios computed as the natural logarithm of mean selection strength in disturbed conditions over mean selection strength in natural conditions, yielding one data point per trait. We then modelled variation in effect sizes as a function of grouping classes (listed in Table S1), fitting for each grouping a separate Bayesian mixed model. These models had the equation: $\hat{y}_{ijk} \sim class_i + system_i + e_{ijk}$, where \hat{y}_{ijk} is the effect size measured on the *k*-th trait in the *j*-th system belonging to the *i*-th grouping class (although note that for 'trait type' groupings, class is a property of individual effect sizes rather than systems). Class is a fixed effect with a coefficient estimated for each grouping class, system is a random effect (following a normal distribution with a mean of zero and a variance estimated by the model), and *e*ijk are residuals. We estimated a single variance term for residuals in each model because many grouping classes had two or few systems. Grouping classes with a single system were excluded from models. We recorded the mean and 95% credible intervals of the posterior distribution of estimated fixed effects, namely the mean effect of human disturbance on selection strength for each grouping class. We also fitted similar models to test for an effect of 'types of control population' in experiments ('field native', 'field exotic', or 'laboratory', as described above), using the subset of data originating from experimental studies.

Disturbance had a small negative effect on selection strength across most grouping factors that we examined, although these effects were generally not significant due to the low number of systems per grouping class (Fig. S3). The only noticeable exception to this general trend were harvested systems in which human impacts on selection were measured by partitioning natural from artificial selection (i.e., two of four harvested systems for S and both harvested systems for β; Fig. S3). For experimental studies, the type of control population used to estimate selection in 'natural' conditions possibly had an effect on estimated human impacts (Fig. S4). This effect, however, was opposite to what we initially hypothesized, with laboratory studies showing a significantly-stronger *negative* effect of disturbance on selection strength than in the other two contexts. Therefore, we conclude that the statistically-significant trend reported in the main text of weaker selection in disturbed conditions (when pooling all non-harvested systems) was also the dominant trend when grouping systems based on a variety of system properties, with no study designs, trait types, fitness components, taxa, or disturbance types (other than harvest) obviously departing from this trend.

Supplementary references

- 1. Caruso CM, et al. (2017) What are the environmental determinants of phenotypic selection? A meta-analysis of experimental studies. *Am Nat* 190(3):363–376.
- 2. Kingsolver JG, Diamond SE (2011) Phenotypic selection in natural populations: What limits directional selection? *Am Nat* 177(3):346–357.
- 3. Geraci M (2014) Linear quantile mixed models: The lqmm package for Laplace quantile regression. *J Stat Softw* 57(13):1–29.

Table S1. Number of systems (taxon-disturbance combinations) for which a given coefficient type is available, grouped by either taxonomic group, type of human disturbance, study design, fitness component measured, or the type of trait on which selection was quantified. The numbers in parentheses indicate the total number of coefficients of a given type gathered from those systems. Note that many systems included multiple traits and trait types, such that system number for grouping 'trait type' indicates the number of systems with a least one coefficient of a given trait type. Grouping classes are described above.

Table S2. Results of general(ized) linear mixed models fitted in a maximum likelihood framework, using the R package "lme4" (formula = response $\sim 1 +$ fixed effects + (1|system/trait)). Results indicate the maximum likelihood estimates of fixed effects along with 95% confidence intervals; effects are 'statistically-significant' if their confidence interval does not include zero. Separate analyses were conducted on the full dataset (ignoring observationlevel uncertainty) and on the subset of selection coefficients with standard errors. For the latter, the inverse of squared standard errors was used as weights in the model, which can then be considered a formal meta-analysis. We used three types of models: a gamma GLMM with a log link function (because the distribution of data points is right-skewed), a linear mixed model on log-transformed absolute coefficients, and a linear mixed model on untransformed absolute coefficients. Fixed effect 'disturbance:harvest' is a two-way interaction effect; the sum of this interaction plus the fixed effect 'disturbance' indicates the effect of disturbance on selection strength in harvested systems. Large positive interactions indicate that the sign of the disturbance effect reverses in harvested systems, leading to significantly stronger selection in disturbed than natural conditions. Effects of disturbance type on *|β|* could not be assessed due to data limitations; we thus fit separate models including (H+) or excluding (H-) harvested systems.

Table S3. Results of linear quantile mixed models predicting the effects of disturbance conditions ('natural' vs. 'disturbed'), disturbance type ('other' vs. 'harvest'), and their interaction on maximum selection strength, measured as *|S|* or *|β|*. Results indicate the maximum likelihood estimate of the 99th conditional quantile \pm 95% confidence intervals. Models could only include a single random effect (system); thus, separate analyses were conducted on the full dataset (ignoring non-independence among multiple estimates from the same trait), and on a 'pooled' dataset where each trait has a single (mean) value in either disturbance conditions (thus eliminating within-trait correlations but reducing the size of the dataset considerably). Effects of disturbance type on *|β|* could not be assessed due to data limitations; we thus fit separate models including (H+) or excluding (H-) harvested systems.

Table S4. Results of linear regressions between effect sizes (log response ratios) of disturbance on mean absolute fitness or on the opportunity for selection (using one of the two as the predictor variable) and effects sizes of disturbance on selection strength (the response variable). Each system contributed a single data point (effect size) for each variable such that a LMM was not necessary. Separate regression models were fitted for effect sizes calculated based on *|S|* and *|β|*. Harvested systems were excluded from the analysis. D: disturbed conditions. *I*: opportunity for selection. N: natural conditions. SE: standard error. *w*: mean individual (absolute) fitness.

Figure S1. Hypothetical example in which a human disturbance reduces the mean absolute fitness of a population of three individuals from 20 to 15 fitness 'units'. If fitness loss is in purely absolute terms (e.g., all individuals produce 5 fewer offspring; scenario 1 below), then the variance in absolute fitness remains constant and the reduction in mean absolute fitness increases the variance in relative fitness (the opportunity for selection). This is the scenario depicted in Fig. 1B of the main text. In contrast, when fitness loss is purely proportional (e.g., all individuals lose exactly 25 % of their absolute fitness; scenario 2), then the variance in absolute fitness decreases just as much as mean absolute fitness, and the opportunity for selection remains unchanged. If fitness loss is proportional but includes some variation (e.g, individuals loose between 10 and 40% of their absolute fitness; scenario 3), then the opportunity for selection can either increase or decrease. More complex scenarios such as negative feedbacks with decreasing fitness (e.g., mortality or reproductive failure at very low absolute fitness) or fitness loss that correlates with individual absolute fitness (e.g., truncation of upper or lower portion of distribution) would also influence the opportunity for selection.

Disturbed conditions

Figure S2. Maximum selection strength (measured as |*S*| or |*β*|) averaged by system or by trait and by disturbance conditions (distinguishing harvested from non-harvested systems). Each line corresponds to a system or a trait. Gray lines are systems or traits for which disturbed conditions represent a disturbance other than harvest. Red lines are for harvested systems/traits, and dotted lines correspond to the subset of those that are fisheries (cod and pike). Circles indicate the mean taken across all systems or traits of a given disturbance type, in the corresponding disturbance conditions. Red and blue symbols respectively correspond to the mean of red and grey lines (harvest vs. other disturbance). Error bars = s.e.m.

Figure S3. Effect of disturbance on selection strength across a variety of system properties. An effect size (log response ratio) of disturbance was calculated for each trait, after averaging coefficients for traits with multiple estimates per disturbance conditions, and then analyzed with Bayesian mixed models including system as a random effect. Separate models were fitted for the five different groupings (taxon, disturbance, experimental design, fitness component, and trait type) and two types of selection coefficients (*S* and *β*). Symbols represent the estimated posterior means with 95% credible intervals; symbols left of the vertical dotted line are grouping classes for which selection was weaker in disturbed than in natural conditions. Open symbols show the mean effect size for grouping classes with a single system, which were excluded from models. The small numbers denote the number of systems (and effect sizes) in each grouping class. Note that for *S*, the two systems with a 'selection partitioning' design are the two fisheries (while for *β* these include one fishery and one mammalian population).

Figure S4. Effect of disturbance on selection strength in experimental studies, grouped based on the type of control population used to measure selection in natural conditions. Open symbols are effect sizes, i.e. log response ratios of selection strength in disturbed vs. natural conditions for individual traits. Positive values on the y axis indicate traits for which disturbance increased selection strength while negative values indicate traits for which disturbance decreased selection strength. Filled symbols with error bars indicate the results of Bayesian mixed models (mode and 95% credible intervals of posterior distributions) estimating mean values in each context. Human impacts on selection strength were estimated using either selection differentials (left) or gradients (right).

Figure S5. Hypothetical example of selection in control (black) and disturbed (red) conditions, showing how human impacts on selection strength (the slope of a line) can vary among fitness components and traits. In the top panel, a human disturbance weakens selection on trait A via mating success, but that same disturbance strengthens selection even more (on the same trait) via another fitness component (survival). In the bottom panel, the same disturbance that weakens selection on trait A via mating success also strengthens selection on trait B via the same fitness component.

standardized trait value

Data sources

Baucom RS, Mauricio R (2004) Fitness costs and benefits of novel herbicide tolerance in a noxious weed. *Proc Natl Acad Sci USA* 101(36):13386–13390.

Calsbeek B, Lavergne S, Patel M, Molofsky J (2011) Comparing the genetic architecture and potential response to selection of invasive and native populations of reed canary grass. *Evol Appl* 4(6):726–735.

Candolin U, Salesto T, Evers M (2007) Changed environmental conditions weaken sexual selection in sticklebacks. *J Evol Biol* 20(1):233–239.

Candolin U, Vlieger L (2013) Estimating the dynamics of sexual selection in changing environments. *Evol Biol* 40(4):589–600.

Carlson SM, et al. (2007) Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). *Ecol Lett* 10(6):512–521.

Carlson SM, Hendry AP, Letcher BH (2004) Natural selection acting on body size, growth, rate and compensatory growth: An empirical test in a wild trout population. *Evol Ecol Res* 6(7):955– 973.

Chávez-Pesqueira M, Núñez-Farfán J (2016) Habitat fragmentation changes the adaptive value of seed mass for the establishment of a tropical canopy tree. *Biotropica* 48(5):628–637.

Dibattista JD, Feldheim KA, Gruber SH, Hendry AP (2007) When bigger is not better: Selection against large size, high condition and fast growth in juvenile lemon sharks. *J Evol Biol* 20(1):201–212.

DiBattista JD, Feldheim KA, Garant D, Gruber SH, Hendry AP (2011) Anthropogenic disturbance and evolutionary parameters: A lemon shark population experiencing habitat loss. *Evol Appl* 4(1):1–17.

Flores-Prado L, Pinto CF, Rojas A, Fontúrbel FE (2014) Strong selection on mandible and nest features in a carpenter bee that nests in two sympatric host plants. *Ecol Evol* 4(10):1820–1827.

Franks SJ, Pratt PD, Dray FA, Simms EL (2008) Selection on herbivory resistance and growth rate in an invasive plant. *Am Nat* 171(5):678–691.

Franks SJ, Wheeler GS, Goodnight C (2012) Genetic variation and evolution of secondary compounds in native and introduced populations of the invasive plant *Melaleuca quinquenervia*. *Evolution* 66(5):1398–1412.

Frei ER, Ghazoul J, Pluess AR (2014) Plastic pesponses to elevated temperature in low and high elevation populations of three grassland species. *PLoS One* 9(6).

Gallagher MK, Campbell DR (2017) Shifts in water availability mediate plant–pollinator interactions. *New Phytol* 215(2):792–802.

Gifford ME, Robinson CD, Clay TA (2017) The influence of invasive fire ants on survival, space use, and patterns of natural selection in juvenile lizards. *Biol Invasions* 19(5):1461–1469.

Hendry AP, Letcher BH, Gries G (2003) Estimating natural selection acting on stream-dwelling Atlantic salmon: Implications for the restoration of extirpated populations. *Conserv Biol* 17(3):795–805.

Jiménez-Lobato V, et al. (2018) Changes in floral biology and inbreeding depression in native and invaded regions of *Datura stramonium*. *Plant Biol* 20(1):214–223.

Kvalnes T, et al. (2016) Harvest-induced phenotypic selection in an island population of moose, *Alces alces*. *Evolution* 70(7):1486–1500.

Lau J, Shaw RG, Reich PB, Tiffin P (2010) Species interactions in a changing environment: Elevated CO2 alters the ecological and potential evolutionary consequences of competition. *Evol Ecol Res* 12:435–455.

Lau JA (2008) Beyond the ecological: Biological invasions alter natural selection on a native plant species. *Ecology* 89(4):1023–1031.

Lau JA, Shaw RG, Reich PB, Shaw FH, Tiffin P (2007) Strong ecological but weak evolutionary effects of elevated CO2 on a recombinant inbred population of *Arabidopsis thaliana*. *New Phytol* 175(2):351–362.

Lopez-Gallego C, O'Neil P (2014) Genetic variation and the potential response to selection on leaf traits after habitat degradation in a long-lived cycad. *Evol Ecol* 28(4):775–791.

Mooney EH, McGraw JB (2007) Alteration of selection regime resulting from harvest of American ginseng, *Panax quinquefolius*. *Conserv Genet* 8(1):57–67.

Murren CJ, Chang CC, Dudash MR (2009) Patterns of selection of two North American native and nonnative populations of monkeyflower (Phrymaceae). *New Phytol* 183(3):691–701.

Murúa M, Espinoza C, Bustamante R, Marín VH, Medel R (2010) Does human-induced habitat transformation modify pollinator-mediated selection? A case study in *Viola portalesia* (Violaceae). *Oecologia* 163(1):153–162.

O'Donnell KL, Pigliucci M (2010) Selection dynamics in native and introduced *Persicaria* species. *Int J Plant Sci* 171(5):519–528.

Olsen EM, Heupel MR, Simpfendorfer CA, Moland E (2012) Harvest selection on Atlantic cod behavioral traits: Implications for spatial management. *Ecol Evol* 2(7):1549–1562.

Olsen EM, Moland E (2011) Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. *Evol Ecol* 25(3):695–710.

Rose E, Paczolt KA, Jones AG (2013) The effects of synthetic estrogen exposure on premating and postmating episodes of selection in sex-role-reversed Gulf pipefish. *Evol Appl* 6(8):1160– 1170.

Saikkonen A, Kekäläinen J, Piironen J (2011) Rapid growth of Atlantic salmon juveniles in captivity may indicate poor performance in nature. *Biol Conserv* 144(9):2320–2327.

Sandring S, Riihimäki M-A, Savolainen O, Ågren J (2007) Selection on flowering time and floral display in an alpine and a lowland population of *Arabidopsis lyrata*. *J Evol Biol* 20(2):558–567.

Sletvold N, Ågren J (2016) Experimental reduction in interaction intensity strongly affects biotic selection. *Ecology* 97(11):3091–3098.

Totland Ø (1999) Effects of temperature on performance and phenotypic selection on plant traits in alpine *Ranunculus acris*. *Oecologia* 120(2):242–251.

Weber A, Kolb A (2011) Evolutionary consequences of habitat fragmentation: Population size and density affect selection on inflorescence size in a perennial herb. *Evol Ecol* 25(2):417–428.

Weese DJ, Gordon SP, Hendry AP, Kinnison MT (2010) Spatiotemporal variation in linear natural selection on body color in wild guppies (*Poecilia Reticulata*). *Evolution* 64(6):1802– 1815.

Wright JT, Gribben PE, Byers JE, Monro K (2012) Invasive ecosystem engineer selects for different phenotypes of an associated native species. *Ecology* 93(6):1262–1268.

Zabel RW, Williams JG (2002) Selective mortality in chinook salmon: What is the role of human disturbance? *Ecol Appl* 12(1):173–183.

We also extracted anthropogenic selection coefficients from the following references, but these had to be discarded from the analysis due to a lack of 'natural' coefficients:

Anderson JH, Faulds PL, Atlas WI, Pess GR, Quinn TP (2010) Selection on breeding date and body size in colonizing coho salmon, *Oncorhynchus kisutch*. *Mol Ecol* 19(12):2562–2573.

Gómez-González S, Torres-Díaz C, Bustos-Schindler C, Gianoli E (2011) Anthropogenic fire drives the evolution of seed traits. *Proc Natl Acad Sci USA* 108(46):18743–18747.

Kendall NW, Quinn TP (2012) Quantifying and comparing size selectivity among Alaskan sockeye salmon fisheries. *Ecol Appl* 22(3):804–816.

Pease KM, Wayne RK (2014) Divergent responses of exposed and naive Pacific tree frog tadpoles to invasive predatory crayfish. *Oecologia* 174(1):241–252.

trait	conditions	selection coefficient	standard error
body mass	Harvest	0.0331	0.0441
horn length	Harvest	-0.0234	0.047
horn base circumference	Harvest	0.0477	0.0496
body mass	Harvest	0.0503	0.0398
horn length	Harvest	0.0076	0.0385
horn base circumference	Harvest	-0.026	0.043
body mass	Harvest	0.0539	0.0349
horn length	Harvest	-0.0413	0.0337
horn base circumference	Harvest	0.0434	0.0364
body mass	Harvest	0.0334	0.0307
horn length	Harvest	0.0039	0.031
horn base circumference	Harvest	0.0303	0.0325
body mass	Harvest	$-7.00E-04$	0.0453
horn length	Harvest	-0.1907	0.0805
horn base circumference	Harvest	0.1655	0.0805
body mass	Harvest	0.1215	0.0359
horn length	Harvest	-0.1755	0.0449
horn base circumference	Harvest	0.0368	0.0426
body mass	Harvest	0.0364	0.0338
horn length	Harvest	-0.1189	0.0397
horn base circumference	Harvest	0.0057	0.0392
body mass	Harvest	-0.0081	0.0393
horn length	Harvest	-0.0547	0.0385
horn base circumference	Harvest	0.0154	0.0365
body mass	No Harvest	0.4376	0.1099
horn length	No Harvest	-0.1238	0.1016
horn base circumference	No Harvest	-0.1014	0.1136
body mass	No Harvest	0.3824	0.131
horn length	No Harvest	-0.2306	0.1065
horn base circumference	No Harvest	-0.1338	0.1265
body mass	No Harvest	0.2365	0.0765
horn length	No Harvest	-0.0043	0.076
horn base circumference	No Harvest	-0.1356	0.0711
body mass	No Harvest	0.1508	0.0962
horn length	No Harvest	0.0159	0.0797
horn base circumference	No Harvest	-0.1557	0.0821
body mass	No Harvest	0.206	0.2021
horn length	No Harvest	-0.3354	0.3651

Finally, we also obtained unpublished data on harvest-induced selection in bighorn sheep (Ovis Canadensis) *from Gabriel Pigeon and Marco Festa-Bianchet (Université de Sherbrooke, Canada). These data, also included in the selection database, were the following:*

