How strong is natural selection?

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The strength of selection in nature has long been a controversial subject, partly because there were few quantitative measurements of phenotypic selection available until recently. In a new paper, Kingsolver and colleagues reviewed 63 studies and found that the median standardized directional selection gradient (a measure of the strength of phenotypic selection) was 0.16. Whether this means selection in nature is strong or weak depends both on one's point of view and on the error in selection estimates.

The ability of natural selection to produce exquisite adaptations of organisms to the environment continues to enthrall us. Evolutionary biologists interested in the mechanisms of adaptation want to know just how powerful natural selection can be within a single generation. The only comprehensive review of natural selection in the wild was Endler's 1986 book[1], but this came just after Lande and Arnold[2] revolutionized the field in 1983 with their widely applicable method of quantifying natural selection. This method led to an explosion of studies measuring the strength of selection in the late 1980s and 1990s. The results of these more recent studies had not been reviewed and synthesized until now. A new paper by Joel Kingsolver and colleagues[3] gives us a far better picture of the data to date, with some discouraging results.

Determining the strength of selection in nature

The methods of Lande and Arnold for measuring selection are conceptually simple[4]. Some measure of fitness (e.g. survival, mating success or lifetime offspring production) is regressed on the phenotypic trait(s) of interest, and the slope of this regression is the estimate of the strength of selection. Linear regression terms measure directional selection, and quadratic (squared) terms measure the amount of curvature in the relationship, including stabilizing and disruptive selection. These estimates are called 'selection differentials', if they include indirect selection caused by

phenotypic correlations, or 'selection gradients', if multiple regression is used to remove indirect selection from the estimate. Both metrics can be expressed in trait standard deviations, so that the strength of selection on any trait in any organism can be readily compared. These methods have now been applied to a wide variety of organisms, providing a substantial body of data on the strength of phenotypic selection using a standardized metric.

Kingsolver and colleagues searched the 16 major journals that publish the majority of measurements of selection. They used stringent criteria to ensure that the studies reflected the strength of selection in the wild, and their resulting database was cross checked in several ways to ensure accuracy. In total, they analyzed 63 different studies of 62 species that included over 2500 estimates of selection; the multiple estimates per study resulted from counting each type of estimate for each trait separately. These studies were approximately evenly split between plants, invertebrates and vertebrates. As Endler found in 1986, the traits measured were heavily biased toward morphology (>80%), with most of the remainder being phenology or life-history traits.

Is selection strong or weak?

The overall impression that the Kingsolver *et al.* paper gives is quite different from that given in Endler's book, but this difference might be based more on reactions to prevailing views at the time each was written rather than on differences in the data. Endler stressed that selection can be quite strong, in contrast to the prevailing assumption in 1986 that selection was extremely weak. This view of strong selection has gained fairly wide acceptance since then. Perhaps in reaction to this, Kingsolver *et al.* now stress the weakness of selection overall. The absolute values of the selection gradients in both reviews had a negative exponential distribution, with many small values and a median absolute value of 0.16 for linear selection and 0.10 for quadratic
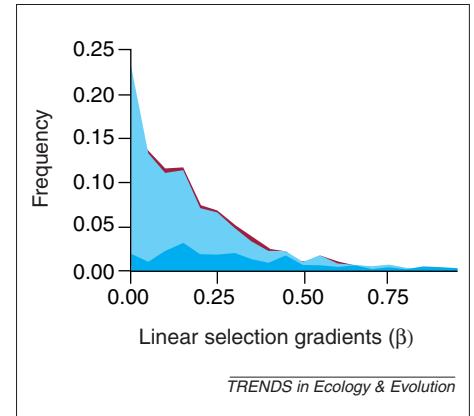

Fig. 1. Frequency distribution of the absolute values of linear selection gradients (β) binned at 0.05 value intervals ($N = 993$). Shading indicates statistical significance (dark blue, significant; mid-blue, nonsignificant; red, not indicated). Reproduced, with permission, from Ref. 3.

in the new data set (Fig. 1). These medians are probably biased upward by a 'file-drawer' effect, where studies without significant selection remain unpublished, and by investigators choosing species and traits for which there is an *a priori* expectation of strong selection.

The exponential distribution, with a long tail containing some quite high values, also agrees with Endler's earlier emphasis that selection can be strong. But here is where the unsettling aspect of this analysis appears. Figure 2 shows the distribution of linear selection gradient estimates in relation to sample size. Note that the large values only occur at the smaller sample sizes and that, above $N = 1000$, most estimates are <0.1. A very similar pattern occurs for quadratic selection gradients. This raises the very real possibility that the long tail of the distribution in Fig. 1 is only the result of estimates with very large error. It seems probable that most of the large and significant estimates of selection in Fig. 2 have 95% confidence intervals that include small values.

However, it would be unwise to take the average strength of selection in only the largest studies and conclude that this is representative of selection in nature. There are only a handful of such studies, and they are probably all on plants. Therefore, even with many studies, we
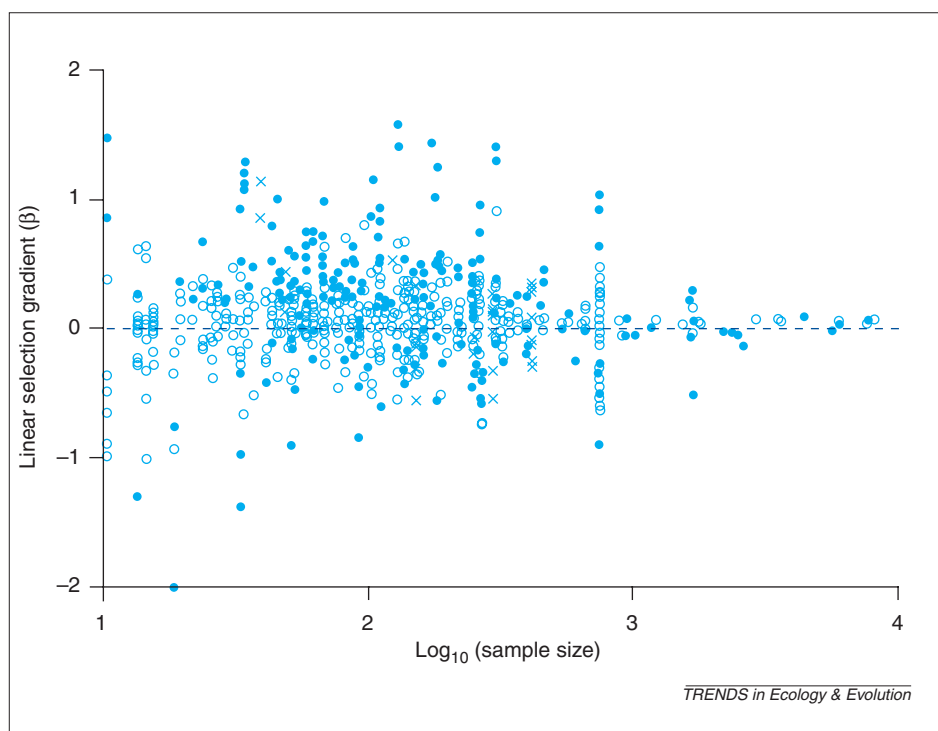
Fig. 2. The 993 linear selection gradient estimates (β) versus sample size. Filled dots are significant at $P<0.05$, open dots are not significant, and X denotes significance not reported at the 5% level. Reproduced, with permission, from Ref. 3.

still do not really know how strong selection is in the wild.

Discussion of strong or weak depends on your definition of these relative terms. The median standardized linear selection gradient of 0.16 in Kingsolver *et al.*'s study, which is commonly considered weak, means that an increase or decrease of one standard deviation in a trait was associated with a 16% increase in relative fitness. Assuming no effects of correlated traits (i.e. no indirect selection) and a heritability of 0.25, selection of this magnitude would cause the trait to change by one standard deviation in only 25 generations, so perhaps this is not such weak selection after all. As a more concrete example, Johnston[5] reported much stronger selection than this on height in the plant *Lobelia*, but, even using the values above, the average height in the population would increase from 56 to 83 cm in 25 generations!

Patterns of selection
The analysis reveals significantly stronger selection on morphological traits than on phenological and life-history traits. Kingsolver *et al.* suggest that this could either be real, or a result of less measurement error for morphology. Similarly, they found that sexual selection is significantly stronger than is viability

selection, which is predicted by some evolutionary theory. However, there could also be a bias introduced by investigators choosing to measure sexual selection on species with strong sexual dimorphism for secondary traits.

Potentially the most surprising pattern uncovered by the analysis is the equal frequency of positive and negative quadratic gradients. Because stabilizing and disruptive selection produce negative and positive quadratic gradients respectively, the equal frequency of these suggests that stabilizing selection is no more common than disruptive selection. Endler[1] also found that stabilizing selection was not particularly common, but he reported more negative than positive quadratic gradients. This result runs counter to the central importance of stabilizing selection in evolutionary theory, and if it holds true, would require some major rethinking. However, if fitness peaks tend to be broad, then stabilizing selection is expected to be weak. For a given sample size, there is less power to detect quadratic than linear terms, so it might just be that the standard errors of the quadratic estimates are so large that it will be difficult to detect a pattern of weak stabilizing selection. In addition, stabilizing selection might be obscured by environmental correlations in ways that

might not apply to disruptive selection[6], and investigators might have chosen traits for which there was an expectation of directional rather than of stabilizing selection.

Back to the future
The results of Kingsolver and colleagues raise several important questions and point the way toward future priorities for understanding natural selection in the wild. One question is why, in the 15 years since Endler pointed out the need for more studies on nonmorphological traits, were >80% of the selection estimates for morphology? The paramount reason is undoubtedly that morphological traits are the easiest to measure, but there might also be other factors, such as a difference in scientific cultures between evolutionary biologists and physiologists. Fortunately, this particular culture clash seems to be waning[7].

The likelihood that most measurements of selection have large standard errors means that, despite the many studies of directional selection on morphology, we might still not have a good idea of the strength of that selection. Intrepid empiricists need to conduct more studies with sample sizes of >1000. More theoretical exploration of power would be useful, as well as resampling from those few datasets with $N >1000$ to recalculate strengths of selection using various sample sizes.

The finding that stabilizing selection was not more common than disruptive selection should stimulate new empirical and perhaps theoretical work. Kingsolver *et al.* suggest that empiricists should measure selection on traits where stabilizing selection is expected based on knowledge of trait function, and once again, use large sample sizes to overcome power and bias problems[8]. The problem of environmental correlations obscuring stabilizing selection could be overcome by using Rausher's[9] method of measuring selection on breeding values; however, it is extremely difficult to get large sample sizes of breeding values.

Despite the stimulating set of analyses conducted by Kingsolver *et al.*, and the importance of the conclusions that they draw, it might be that the most important impact of this work will be from the data base that they have created. This data base will be available online at http://www.bio.unc.edu/faculty/kingsolver/, and

will allow other researchers to perform their own analyses and answer different questions. This might prove to be the most important long-term legacy of this ground-breaking study.

References
1 Endler, J.A. (1986) *Natural Selection in the Wild*, Princeton University Press
2 Lande, R. and Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution* 37, 1210–1226
3 Kingsolver, J.G. *et al.* (2001) The strength of phenotypic selection in natural populations. *Am. Nat.* 157, 245–261
4 Brodie, E.D., III *et al.* (1995) Visualizing and quantifying natural selection. *Trends Ecol. Evol.* 10, 313–318
5 Johnston, M.O. (1991) Natural selection on floral traits in two species of *Lobelia* with different pollinators. *Evolution* 45, 1468–1479
6 Price, T. *et al.* (1988) Directional selection and the evolution of breeding date in birds. *Science* 240, 798–799
7 Dudley, S.A. (1996) Differing selection on plant physiological traits in response to environmental water availability: a test of adaptive hypotheses. *Evolution* 50, 92–102
8 Travis, J. (1989) The role of optimizing selection in natural populations. *Annu. Rev. Ecol. Syst.* 20, 279–296
9 Rausher, M.D. (1992) The measurement of selection on quantitative traits: Biases due to environmental covariances between traits and fitness. *Evolution* 46, 616–626

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Paving the way to the future of Amazonia

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The fate of the Brazilian Amazon is threatened by a new wave of frontier expansion following new infrastructure commitments worth US$40bn from the federal Government. In a recent paper, alarming rates of deforestation and forest degradation have been predicted, which could be either pessimistic or optimistic depending on the scale of forest disturbance being considered. A more decisive preventative approach is needed to prevent further impoverishment of both the biota and rural population of Amazonia.

Brazilian Amazonia incorporates nearly 40% of the remaining tropical rainforests of the world, making it by far the largest tropical forest region under the jurisdiction of a single nation; nowhere else is forest loss occurring faster in absolute terms. Although the cumulative area cleared so far is 550 000 km^2 or 14% of the total forest cover of the region, deforestation rates between 1995 and 1999 averaged 1.9×10^6 ha yr^{-1}, not including clearings smaller than 6.25 ha and extensive areas of forest disturbed by selective logging and ground fires[1].

These smaller scales of disturbance, although largely invisible to conventional satellite imagery, can lead to irreversible ecosystem transitions. For example, recent El Niño events have breached the forest flammability threshold of the one-third of Amazonia that repeatedly experiences strong seasonal droughts, particularly in areas where soil water retention capacity is low[2]. Although the total forest area burned following exceptionally prolonged dry seasons remains unknown, wildfires in such years might release as much carbon as is released from deliberate deforestation[3].

With El Niño events becoming increasingly more frequent and severe[4], the probability of accidental wildfires is further aggravated by logging operations, which puncture the canopy and increase the understorey fuel load[2,5]. Once a closed-canopy forest succumbs to an initial surface fire (Fig. 1), more intensive recurrent burns in a fire-intolerant system are likely to drive rapid changes in forest structure and composition that will

Fig. 1. The threat of fire. In seasonally dry areas of the Amazon, surface fires that originate in nearby cattle pastures and slash-and-burn plots pose a serious threat to forests. Photograph reproduced, with permission, from M.A. Cochrane.

drastically reduce the biodiversity, hydrological and carbon-retention value of the resulting ecosystem[2,6,7].

Avança Brasil
Time is rapidly running out for the effective implementation of a comprehensive network of conservation areas retaining undisturbed forest cover, particularly along frontier regions where much of the deforestation process is concentrated. This is all the more urgent given the sheer scale of infrastructure commitments earmarked by the Brazilian Government for the region under the auspices of the Avança Brasil (Forward Brazil) development scheme. Avança Brasil is a massive investment program, worth US$40bn (to be spent by 2008), including new all-weather highways, railroads, pipelines, hydroelectric dams, power lines, river-channelization projects and new port facilities[8]. The paved-road network alone in the region is expected to more than double, with about 7500 km of new paving (W.F. Laurance, pers. commun.), providing heavily subsidized access to many previously remote parts of the region for the timber, mining and agricultural sectors. Current estimates of the amount of forest that will be cleared in the next 25–35 years within a 50-km strip on either side of four highways alone range from 80 000 km^2 (Ref. 9) to 270 000 km^2 (Ref. 10). According to the Brazilian Planning Ministry, this is 'the shortest way to the future'[8], whatever that future might be.

Part of the economic logic for paving the southern Amazonian highways comes