In recent years, the fluctuation relations have been, first tested, and later used to interpret experimental results.

Early tests include the fluctuations in current or voltage across a resistor in an electrical circuit and the fluctuations of a torsion-pendulum immersed in a fluid. For the latter one considers a small mirror suspended in a fluid and attached to a thin wire with torsional stiffness C. The mirror together with the surrounding fluid has an effective moment of inertia I_{eff} and it is driven out of equilibrium by applying a time-dependent external torque $M(t)$

The deflection $\theta(t)$ of the mirror is recorded as a function of time. The dynamics of the deflection angle $\theta(t)$ follow from a Langevin equation

$$I_{eff}\,\ddot{\theta}(t) + \eta\,\dot{\theta}(t) + C\,\theta(t) = M(t) + \sqrt{2\eta k_B T}\,\xi(t)$$

where η is the fluid viscosity and $\xi(t)$ a white noise term. Experiments showed that the fluctuation relation

$$\frac{p(W)}{p(-W)} = e^{W}$$

applies for the work W as long as the work is integrated over a sufficiently long time Δt

Another nice application comes from the study of molecular motors where it was found that the accumulated rotational angle Θ_t of a molecular motor opperating for a time t follows the fluctuation relation

$$\frac{p(\Theta_t)}{p(-\Theta_t)} = \exp\left(\frac{M\Theta_t}{k_B T}\right)$$

which allows to calculate the torque M of the motor by recording the experimentally more accessible statistics of rotations $p(\Theta_t)$.

We derived the fluctuation relations from a Langevin description with δ-correlated noise, or more generally from a Markovian description of the microscopic dynamics. This implies that they will only be valid on time-scales large compared to the microscopic time-scale of the physical system. The Crooks relation generically has the form

$$\frac{p(A)}{p(-A)} = \exp\left(-\frac{NAt}{k_B T}\right)$$

where A is some observable and N is the particle number. Due to the exponential the right hand side quickly becomes immeasurably small for

(i) Large values of the observable A
(ii) Large particle numbers N
(iii) Long times t

All of these limit the observability of the fluctuation relation in experiments

(i) We would like to concentrate on small values of A, but we are limited due to measurement errors.
Moreover, for the case of, say, very small typical heat exchange, we are back to a system close to thermal equilibrium. This is not what we wanted to study

(ii) Small numbers of particles in a system may not easily be obtained or may not be a case of interest

(iii) Short integration times demand high resolution measurements. Moreover we are still limited to times large compared to the microscopic time scale

So far all apparent failures of the fluctuation relations could be traced back to implicit violations of one or more of these conditions

Evolution and Fluctuation Relations

V. Mustonen, and M. Lässig, PNAS 107, 4248 (2009)

Consider a population with a wild type and a mutant and denote the fraction of mutants $x = x(t)$ as it is expected to change over time

The difference in reproduction rate between mutant and wild type is called selection coefficient $s = s(x,t)$

If the selection coefficient does not explicitly depend on time we can think of it as being the gradient of a fitness $F(x)$, i.e.

$s(x) = \partial_x F(x)$

The graph of $F(x)$ is often called a fitness landscape in analogy to the potential energy landscape of physical systems. If we assume random mutations to occur in an uncorrelated fashion we arrive at a Langevin equation for $x(t)$

$$\partial_t x = \partial_x F + \xi$$

with a white nois ξ

Let's call the distribution of x in the absence of selection $P_0(x)$.

One defines a fitness flux

$$\Phi[x(\tau)] := \int_0^t d\tau \, s(x(\tau), \tau) \, \dot{x}(\tau) = \int_{x(0)}^{x(t)} dy \, s(y, t(y))$$

which in the case of $s = s(x)$ is given by

$$\Phi[x(\tau)] = \int_{x(0)}^{x(t)} dy\, s(y) = \int_{x(0)}^{x(t)} dy\, \partial_y F(y) = F(x(t)) - F(x(0))$$

i.e., just the difference of fitness.

For a time-dependent selection coefficient $s(x,t)$ which, in analogy to rolling waves, has been likened to a fitness seascape, one can derive a Crooks-Relation

$$\frac{p[\hat{x}(\tau)]}{p[x(\tau)]} = \exp\left[-N\Phi[x(\tau)] + \Delta H\right]$$

where N is the population size and $H(x,t) := \ln \frac{P(x,t)}{P_0(x)}$ is the log-liklihood of x at time t. The fitness flux, therefor, takes the role of the trajectory-dependent heat, and ΔH the role of a free energy difference. One consequence is a 2nd law-like relation

$$N\langle\Phi\rangle \geq \Delta H,$$

i.e, the fitness flux is bounded from below. Moreover, even if $\Delta H = 0$, i.e., there is no evolutionary drift, the fitness flux cannot be negative, i.e. fitness will not (on average) decrease.