

Equilibrium, the new dirty word of ecology

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Natural systems are always fluctuating: no two years are identical, with population and community sizes varying from one year to the next. Such variation has led to “equilibrium” becoming almost a dirty word in ecology. Some researchers see the world as being in permanent flux, and consider our field’s historical focus on equilibria as out-dated. But this view is flawed, is driven by current day observations of a world out of kilter, and risks downplaying the risks of ongoing anthropogenic change to civilisation and perhaps too to life on Earth. In this viewpoint, I mount a defence for equilibria.

In 1972 Eldredge and Gould introduced the concept of punctuated equilibrium where species remain in evolutionary stasis for most of their history (Gould & Eldredge 1972). The focus on protracted periods of stasis opposed the then dominant view of gradualism, where species are constantly changing (Erwin & Anstey 1995). We now know that many fossil records do exhibit punctuated equilibrium, and this does suggest that the natural state of natural systems is relative constancy (Hunt *et al.* 2015). Work on ancient community structure also suggests stasis, with species composition remaining constant for centuries, millennia, or even longer (Barnosky *et al.* 2016). Constant community structure and evolutionary stasis means no one species grows to become dominant driving competitors extinct, and that successful invasions are unusual.

The problem with the concept of equilibria in ecology is two-fold: first, the way many ecologists define it, and second that we currently live in a world that is not at equilibrium as a direct result of our behaviour. The equilibrium we are first taught in college is of a population that is unchanging in size, such as that predicted by the continuous time logistic equation of population growth once carrying capacity is achieved (Begon *et al.* 1986). The modelled population settles to a constant size that never changes, and this is the equilibrium that many empiricists picture when they hear equilibria discussed. However, this equilibrium is a deterministic equilibrium, and it is just one form of equilibria. A stochastic, density-dependent, equilibrium occurs when a population fluctuates with size, but shows no long-term temporal trend in its size, or in the magnitude or frequency of fluctuations (Coulson 2012). A population that is at a stochastic equilibrium is said to be “stationary”.

Strictly speaking, things are even more complicated. The deterministic and stochastic equilibrium in the paragraph above describe population size as being at equilibrium. But a population that increases, or decreases, in size at a constant deterministic, or stochastic, rate, is also considered to be at equilibrium (Tuljapurkar & Caswell 2012). In these cases, the equilibrium describes the population growth rate. When population size is at a deterministic equilibrium, the population growth rate is zero, and when population size is at a stochastic equilibrium the long-run stochastic population growth rate is zero.

Theoretical biologists usually appreciate the wide variety of equilibria that exist, and this appreciation has led to biologists developing a deep understanding of both deterministic

and stochastic equilibria. For a community to be ecologically and evolutionarily stationary, there must be no persistent long-term trend (say over a minimum of a few hundred time-steps) in species composition, of population size of each species, or in allele (or breeding value) frequencies of each of the species. Strictly speaking, there must be no temporal change in any of the distributions of population size or allele frequencies of each species (i.e. the variances and other moments of the distribution must also remain stationary with time) (Coulson 2020). For this to happen the following conditions need to be met.

1. Long-run stochastic growth rates for all populations in the food web are zero and they exhibit no long-term temporal trend: for any population to have a long-run stochastic growth rate of zero, some factor must be limiting its growth. This occurs when the effects of all antagonistic interactions in the food web are greater than the effects of non-antagonistic interactions such as mutualisms.

2. Genetic variation is maintained and evolution does not occur: for a population to be at evolutionary equilibrium and to maintain additive genetic variation, the alleles or breeding values underlying each trait must be subject to either i) frequency-dependent selection, ii) stabilizing selection with selection-mutation balance, or iii) non-directional negative fluctuating selection, or iv) no selection at all, with population sizes sufficiently large that the effect of drift is negligible. Frequency-dependent selection can be generated via a number of mechanisms including spatial variation in selection pressures, heterozygote advantage, and individual specialisation (Crow & Kimura 1970; Mitchell-Olds *et al.* 2007). In an evolutionarily stationary community, this condition must be met in all species.

3. Competing species on the same trophic level are able to coexist: when a community is stable, coexistence mechanisms must operate between competing species on the same trophic level. Stabilising mechanisms operate when two species on the same trophic level do not have complete overlap in the set of species that influence their population dynamics. Equalizing mechanisms occur when the sign or magnitude of the effects of the same directly interacting species on two competing species on the same trophic level differ. The storage effect and relative non-linearity occur when two competing species are affected in different ways by aspects of the variable abiotic environment (Chesson 1994, 2000).

4. The community matrix that describes the food web has a real part of the dominant eigenvalue that is less than zero (May 1973): the community matrix describes direct interactions between species that are determined by the rate of encounters between individuals of each directly interacting species, and the expected outcome of each encounter (Landi *et al.* 2018). If conditions 1) to 3) are met, then the community matrix describing all direct interactions will be stable.

It may sound implausible that these conditions can be simultaneously met for a food web, and, of course, in reality it is probable that some slow evolution, and coevolution, occurs – i.e. gradualism is not completely dead. However, given observations of constant community structure and apparent evolutionary stasis, such evolution is not sufficient to knock the system away from its stationary state.

The fossil record has revealed that a number of processes can knock communities and ecosystems away from a stationary state (Rytkiel Jr 1985; Coulson 2020). Meteor strikes, volcanic eruptions, and climate change caused by long-term periodicity in the Earth's orbit have been invoked as processes that can do this, but so too has evolutionary innovation. If a species evolves a phenotypic trait that can impact its ecosystem or community, the food web describing the system can be rewired. The evolution of lignin, and the human brain are

evolutionary innovations that have rewired food webs on a global scale (Robinson 1990; Harari 2014).

Although mathematical biologists have a very good understanding of equilibria and stationarity, they have a much poorer understanding of what happens when a tipping point is reached where a system is knocked so far from its stationary state that it is unable to return to it. We are currently, generally, unable to predict the new stationary state a system will achieve following a major perturbation. One of the systems I study, the freshwater communities of Trinidad, exist in two stationary states – one with apex predatory fish, and one without. Interestingly, when predators are removed from the system, the new low-predation stationary state the system eventually achieves is always the same (Reznick *et al.* 2019). This suggests there may, at least in some circumstances, be predictability in what happens when a system is knocked out of kilter.

The potentially very big problem that humanity currently faces, as we all know, is that we have knocked the world, and the majority of communities in it, away from a stationary state, and we know very little about the new stationary states these systems will achieve. We have no idea whether these states will be as supportive of civilisation as the stationary state from which it emerged. My guess is it won't be. We are living in a period of transience, but one that we are studying in considerable detail. But by considering these transient dynamics as normal, we risk forgetting the lessons we have learned by studying stationary systems at equilibrium.

It is my belief that we urgently need to conduct joined-up collaborative research on i) why natural systems typically tend to stationary states, ii) what happens when we perturb them away from those states, and iii) the circumstances when we can predict the new stationary states that will emerge (Coulson 2020). This might help us understand the journey we have set our Earth systems on, and allow us to more effectively plan solutions to help humanity. If we don't do this, we risk finding ourselves in a new stationary we don't very much like. On the plus side, many ecologists and evolutionary biologists are working on aspects of each of the three research areas described above. The challenges are to agree (or not) i) a more nuanced, widely accepted, appreciation of stochastic equilibria and stationarity in ecology, ii) that stationary states are the typical state of natural systems, ii) that a more coherent approach to addressing the questions raised above is a useful avenue to pursue. If we do this, not only might we have taken a useful step towards leaving our descendants a world in a stationary state they wish to inhabit, but we will also might just, end up developing a general theory for the dynamics of natural systems. Seems like a win-win to me.

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