

The "Balance of Nature" metaphor in population ecology: theory or paradigm?

Kim Cuddington

Department of Philosophy
University of Guelph
Guelph, ON
N1G 2W1
Canada

mailing address: Department of Ecology and
Evolutionary Biology
University of Connecticut
75 N. Eagleville Rd., U-43
Storrs, CT 06269-3043
Phone: 860-486-3710
kcudding@uconnvm.uconn.edu

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Abstract

I claim that the "balance of nature" metaphor operates as a shorthand for a paradigm which view nature as a beneficent force. I trace the cultural origins of this concept and demonstrate that it operates today in the discipline of population ecology. Although it might be suspected that this metaphor operated a pre-theoretic description of the more precisely defined notion of equilibrium, I demonstrate that the "balance" concept has been used to define those types of equilibrium which are deemed natural. This interaction suggests that the metaphor is much more than a precursor of the theoretical concept of population equilibrium.

Introduction

The use of metaphors is a ubiquitous part of the scientific process. Boyd (1993) claims that metaphors in science are either pedagogical or theory-constitutive. That is, metaphors are either used to explain theories which already have non-metaphorical explanations (e.g. electron cloud, wormhole), or they are used to express theoretical claims for which there is, as yet, no non-metaphorical formulation. As Black (1962) explains, we need metaphors in those cases where there can be no question as yet of precise scientific statements.

Within the theory-constitutive realm, most authors emphasize the importance of increasing the clarity of scientific metaphors, while admitting that ill-defined metaphors can play a role in the discovery process (Gentner and Jeziorski 1993). However, metaphor is not a substitute for more precise theoretical statements, and as a science or theory matures, its metaphors will be expressed in formal language that subsequently enables predictions.

The "balance of nature" metaphor has influenced the development and continued practice of ecology. The basic concept is powerful, and yet ill defined. When one aspect of it is claimed

to be disproved, or misguided, it reappears like a Hydra, rearing another of its innumerable heads in yet another definition or subdiscipline. Within a subdiscipline, it has been given increasingly precise definitions, but when such definitions are demonstrably false, a new ones arise. I suggest that the “balance of nature” metaphor, when it is invoked in the science of ecology, is neither pedagogical nor theory-constitutive.

Instead, the metaphor expresses a particular way of viewing the natural world, which has little to do with scientific theories or observations. The metaphor is a shorthand for expressing a world view which emphasizes a beneficent interpretation of ecological relationships. However, the maintenance of this paradigm does not rely on merely on scientific inertia and the absence of viable alternatives, as might be suggested by a Kuhnian explanation. The “balance of nature” metaphor is expresses a cultural concept. It has an ancient history, and today influences scientists and non-scientists alike. In ecology, when more precise, non-metaphorical statements of the concept have lead to predictions which do not fit the more naïve metaphor, the theory and not the metaphor has been abandoned. In short, the balance of nature concept embodies our beliefs about the predictability and resilience of nature.

Historical Background

The idea that there is balance in nature is part of most cosmologies (Egerton 1973). In western thought, the concept of balance of nature was a central theme of ancient natural history. All things were believed to be interconnected to preserve an order. Historically, this order was described as pre-ordained by a divine power, randomness and extinction of species were not normally considered possibilities, and variation and change were largely ignored (Kingsland 1985). Herodotus explained the persistence of prey species by noting that each predator and prey species had been providentially supplied with differentiated reproductive capacities (Egerton

1973). Cicero claimed that the persistence of species expressed the wisdom and benevolence of the creator (Cicero 1938).

In more recent times, prior to Darwin, it was thought that unity and harmony were imposed on the world by a benign creator. William Paly found evidence for the existence of God in the design of Nature. Although Darwin effectively removed the argument from design from the field of natural history, the concept of balance infuses parts of *The Origins* (Egerton 1973). The “balance of nature” metaphor was first reinterpreted in a Darwinian context by Herbert Spencer. Spencer reasoned that the preservations of races implied a stable equilibrium between destructive and conservative forces (Kingsland 1985).

The ancient history of the “balance of nature” metaphor is by no means a proof that it is not operating in a theory-constitutive manner, although it is clearly not pedagogical. However, early in the history of ecology, this metaphor implied that nature was orderly and beneficent, perhaps in the same way that the, now absent, divine presence had been similarly benign. The balance of nature concept was whole-heartedly embraced by Forbes, an influential founding member of the new science of ecology. Forbes merged Darwinian natural selection with Spencerian arguments about balance. He explicitly advanced the idea of the balance of a nature as a "beneficent order" which was promoted by the process of natural selection through competition and predation. These forces established an equilibrium that "is steadily maintained and that actually accomplished for all parties involved the greatest good which circumstances will at all permit" (Forbes 1887).

Clearly, we have thought about nature in terms of balance for a very long time, certainly before ecology was a scientific discipline. In this respect, the metaphor is perhaps operating in a slightly different capacity than other metaphors in science. Similarly, if the metaphor does

encompass a particular world view, its historical origins clearly indicate that it is not merely a scientific paradigm.

The “Balance of Nature” Concept in Population Ecology

Today, the balance of nature metaphor is a powerful force in ecology and related areas. It has been used to spearhead the new science of conservation ecology, and lies at the centre of many environmentalist positions. Within ecology, current research and syntheses address this metaphor and explain how it does or does not apply to population numbers (Andrewartha and Birch 1954), species numbers (Pimm 1991) or community function (McCann et al. 1998). Modern ecology textbooks refer to the ubiquity of balance (Begon et al. 1986), while in the same breath discussing the problems of irregularly fluctuating pest species, and lamenting species extinctions and the destruction of whole ecosystems.

In modern ecology, the balance of nature concept entails the belief that nature operates to strike a balance between disparate forces. The result is a system that experiences community persistence or only small fluctuations in population and species number. We can divide these as: 1) the claim that natural populations have a more or less constant numbers or individuals, 2) the claim that natural systems have a more or less constant number of species and 3) the claim that communities of species maintain a "delicate balance" of relationships.

If we focus on the claim about population numbers, we find that the definition of what constitutes a “balance” in population size has been modified numerous times, but the commitment to balance has never been abandoned, even when a previous definition was demonstrably false. This not an unusual characteristic of scientific theories, and perhaps coincides well with a Kuhnian description of a scientific paradigm. We might be tempted to conclude that the “balance of nature” metaphor served as a pre-theoretic concept for the

mathematical equilibriums described by equations governing populations dynamics. However, I will demonstrate that the interaction between scientists' understanding of "balance of nature" metaphor, and the notion of equilibrium indicate that the metaphor is more than a pre-theoretic concept. Indeed, the metaphor defines the paradigm, and limits the definition of the theoretical entity "equilibrium".

The simple idea of ancient naturalists was that numbers of plants and animals were fixed and in balance, while observed deviations, such as plagues of locusts, were the result of punishments sent by divine powers (Krebs 1994). Even in 1714, Dernheim thought that population numbers were balanced and used ecological examples as evidence of divine wisdom, but claimed that outbreaks of noxious species "serve as Rods and Scorges to chastise us" (Egerton 1973).

After Darwin, population numbers were claimed to be balanced, although the divine no longer figured in these explanations, instead "nature" struck a balance. However, there were some early doubts, in 1855 Wallace mused in an unpublished journal,

"Some species exclude all others in particular tracts. Where is the balance? When the locust devastates vast regions and causes the death of animals and man, what is the meaning of saying the balance is preserved?...To human apprehension there is no balance but a struggle in which one often exterminates another." (Egerton 1973)

In ecology, Stephen Forbes (1887), supported a claim that the balance of nature maintained population numbers at constant levels (Definition 1),

"Perhaps no phenomena of life in such a situation is more remarkable than the steady balance of organic nature, which holds each species within the limits of a uniform average number, year after year..."

He envisioned a balance that occurred by species having evolved a birth rate which matched their death rate, thus producing a steady state. The idea lingered for a long time in ecology, David Lack still felt the need to disabuse his readers of this notion in 1954.

Oddly enough, Forbes worked on the biological control of pest species, where population outbreaks were an economic problem. It is perhaps not surprising that even today insect outbreaks are viewed as an unusual, unnatural and certainly undesirable event. In any case, the claim that there are more or less constant numbers in individuals in a population was clearly false, even in Forbes' experience. Elton, one of the founders of animal ecology was flatly opposed to the balance of nature concept with respect to population numbers:

'The balance of nature' does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude" (Elton 1930).

However, the balance of nature concept had already been redefined by insect ecologists. Howard and Fisk (1911) analyzed populations of gypsy moth and brown fall moth and claimed that these populations were in a state of balance, so that they maintained a constant density if averaged over many years. Nicholson (1933) and Smith (1935) developed this position and claimed that population densities are always changing, but the values tend to vary about a characteristic density. Balance of nature was interpreted as persistence with limited change in population number, so that the overall population retained its essential characteristics (Definition 2).

These verbal descriptions of balance were soon augmented by the more rigorous concept of mathematical equilibrium. Simple models developed in the 20's were used to explain, and less commonly, predict, population dynamics of predator-prey systems. In its early development, mathematical ecology used concepts from physical chemistry. At that time, simple chemical

reactions, conducted under well-mixed conditions, were explained by the approach of the system to stable or equilibrium conditions, where the rate of combination and separation of the reactants was exactly balanced.

Volterra and Lotka, two early theorists, used the idea of equilibrium to describe ecological communities, in particular, predator-prey populations (Kingsland 1985). It is doubtful that Lotka and Volterra were initially influenced by the prevalent assumption in ecology of a harmonious balance of the predator and prey populations. Neither of them were ecologists, and Lotka imagined his work would be read mainly by physicists. Part of the bias for examining only equilibrium conditions was probably due to the fact that the tools for determining the behaviour of systems near equilibrium points had been well understood since the 19th century (e.g. those developed by Henri Poincaré), while there were no reliable techniques for determining the behaviour of these dynamics systems far from equilibrium. From its inception, mathematical ecology has focused on the equilibrium solutions of models describing animal populations.

This notion of equilibrium coheres well with the "balance" metaphor for natural population size. Biotic, density-dependent effects, by altering birth and death rates, served to create an equilibrium population density. Pimm (1991) characterizes this as the "simple equilibrium plus noise model", which posits an equilibrium density to which populations quickly return after inevitable environmental disturbances (noise). This is basically a more precise formulation of Nicholson's definition.

Pimm (1991) asserts that today, ecologists equate the idea of balance of nature with this concept of mathematical equilibrium. However, it is unlikely that the "balance of nature" metaphor was merely a pre-theoretic version of the idea of equilibrium. The balance of nature

metaphor and the more precise definition of equilibrium from mathematical ecology interact, and have done so from the very beginning. Ecologists have tended to reject those types of mathematical equilibrium that don't cohere well with the "balance of nature" metaphor.

The initial models of predator and prey populations that Lotka and Volterra developed predicted sustained oscillations of predators and prey, the magnitude of which were determined by the initial conditions of the systems. However biologists and the modellers themselves quickly asserted that such fluctuations were not present in nature. Volterra developed a theory that distinguished between "dissipative" and "conservative" systems. Conservative systems were defined as analogous to frictionless systems in mechanics where oscillations remained constant. Although an ideal pendulum might swing forever, a real one would certainly not. Natural ecological systems, claimed Volterra, operated in the same way, sustained oscillations of predator and prey populations were not present in the real world (Kingsland 1985).

Interestingly enough, in spite of these claims about the unnatural character of the model predictions, some ecologists were by this time aware of natural systems with sustained oscillations in predator-prey density. Elton's study of was interested in the sustained oscillations of some predator and prey species in the arctic, had inspired many ecologists to look for similar oscillations in other species (see issues of *Journal of Animal Ecology* 1930-1940).

Simple continuous time models of the sort used by Lotka and Volterra do not have as much interesting dynamic behaviour as the discrete time models later developed by early insect ecologists. These population models also exhibit other behaviours such as increasing (rather than stable) oscillations in population density. Unlike Volterra, Nicholson and Bailey, in 1935, were willing to claim that stable oscillations can occur in natural populations. Indeed, there was ample evidence to do so. When they found, however, that their population model also predicted

increasing oscillations in population size which eventually lead to extinction, they claimed that "a probable effect of increasing oscillation is the breaking up of the species-population into numerous small, widely separated groups which wax and wane and then disappear, to be replaced by new groups..." or "large fluctuations produced by increasing oscillations may ultimately be limited by factors other than parasites, so that oscillation is perpetually maintained at a large *constant* amplitude in a constant environment" [italics mine] (Nicholson and Bailey 1935). Clearly, stable oscillations and constant equilibriums were now a "natural" behaviour, but unstable oscillations and extinctions were not. This definition seems to fit with a modern statement about equilibrium,

“Despite this, fluctuations in population size are not unbounded; no population increases without limit and species only occasionally become extinct. One of the central features of population dynamics, therefore, is the simultaneous occurrence of flux and relative constancy” (Begon et al. 1986) (Definition 3).

As well, Nicholson's first claim about the subdivision of populations has been developed into another position, metapopulation theory. This theory suggests that while a predator and prey population may go extinct in one spatial location because of large amplitude fluctuations in density, immigration and emigration, as well as asynchronous occurrences of extinction will create a persistence of larger populations and indeed, small fluctuations in an average density over a large area (Definition 4).

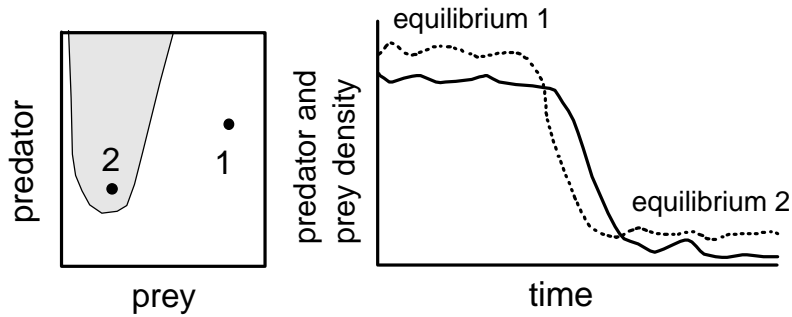
Equilibrium concepts continue to dominate ecological thinking. Hastings et al. (1993) noted that " underlying the focus on stable equilibrium is the assumption that communities in nature correspond at least loosely, to the stable equilibrium of model systems. Predictions of long term behaviours is based on the notion of approach to stable equilibrium."

The “Balance of Nature” Metaphor and the Concept of Population Equilibrium

It is clear that, historically, definitions of the "balance of nature" metaphor in population ecology have been rather slippery. They have had a tendency to be modified to fit disconfirming evidence, and at least four different variations can be identified. It could be claimed that the “balance of nature” concept has now been more precisely defined as the theory that population densities approach and remain at equilibriums of the kind described by predator-prey population models (give or take some environmental variation). If correct, we are compelled to embrace the claim that the balance of nature metaphor operated as a pre-theoretic concept, for which we now have more precise and accurate formulations.

However, this is not an entirely accurate description. Some kinds of dynamic behaviour predicted by mathematical models were assumed not to apply to natural populations. Volterra could not conceive of sustained oscillations in predator-prey density. Nicholson and Bailey thought that extinction was an unlikely outcome of an interaction between predator and prey. Even today, only certain kinds of equilibriums are invoked to explain fluctuations in population densities. While many ecologists may claim that populations are governed by equilibrium dynamics, those equilibrium dynamics which are considered plausible are a very restricted set of biologically possible behaviours.

Models developed in the 60's suggested that populations may have multiple stable states. That is, the initial population densities could determine whether prey populations reached an equilibrium at a low density or at a high density. Further, disturbances to the system could cause a population to flip from one equilibrium state to another (reviewed in May 1977) (Fig. 1). Overall, the notion of multiple stable states is not a well-used concept in ecology even though it is an accepted explanation of some population fluctuations. Most ecologists accept the notion



that multiple stable states are possible (i.e. “natural”), but they usually do not believe that these types of dynamics occur in the populations they study (with the

notable exception of those that work on grazing effects on grasslands). Today fisheries and pest management is predicated on simple models of populations that predict a single stable equilibrium density. Where more complicated models are invoked (e.g. multiple stable states of spruce budworm), they do not appear to affect management strategies in any appreciable degree. Even predictive failure is not enough to move ecologists to consider different types of equilibrium behaviour. Five major commercial fisheries have collapsed to extremely low levels of population density and have not recovered in spite of reduced or suspended fishing activity (Krebs 1994). In spite of this, models with multiple stable states are not a standard part of fisheries management.

However, multiple stable states are relatively well-behaved types of equilibrium behaviour. Bundiansky (1995) claims that early modellers in the 40's and 50's also discovered that their population models could produce chaotic behaviour, but did not consider that this was a "natural" phenomena. In 1974, Robert May published influential articles in *Science* and *Nature* (e.g. May 1974) which demonstrated that very simple population models could exhibit chaotic behaviour under particular parameter conditions. In chaotic systems, asymptotic solutions have the property that two population densities lying close together initially will, in general, diverge over time (i.e. sensitive dependence on initial conditions). Predictions can be made in the very short term, because the system is deterministic; however, over the long term, populations which started out with very similar densities will have different densities and dynamics. And yet, chaos

theory, which has profoundly changed the way we look at physical systems, seems to have barely nudged the consciousness of most practicing ecologists.

Pimm (1991) claims that empirical ecologists lack of interest in chaos can be explained by the effects of an influential paper by Hassell *et al.* (1976). The authors measured the reproductive rates of different insect species and concluded that the majority would be unlikely to exhibit chaotic dynamics. Pimm argues that the authors' conclusions were persuasive and ecologists stopped looking for complex dynamics after the appearance of this paper, and 3 or 4 subsequent papers which used the same technique. One wonders why such a small group of papers completely deadened ecologists' curiosity about a new phenomena, which at the same time was generating waves of interest, controversy and experiments among physicists. One claim is simply that Hassell *et al.* were right, chaos is unlikely to occur in natural biological systems, and empirical ecologists strongly believed this. However, recent studies, undertaken primarily by theoretical ecologists, have found that chaos occurs in a reasonably large percentage of natural populations (Pimm 1991). Yet even now, there are few studies regarding chaotic dynamics in ecological populations, even though a closely allied science, physiology, makes good use of the concept.

I suggest that the reason ecologists today are uninterested in chaotic dynamics and multiple stable attractors is the same reason that Volterra rejected the idea of stable oscillations whose amplitude depended on initial conditions, and Nicholson and Bailey could not conceive of population extinction as a natural outcome of a predator-prey interaction. The balance of nature metaphor does not cohere well with this type of equilibrium behaviour, which is both predicted by population models and found in natural populations. A stable equilibrium density, on the other hand, does cohere well with the notion of “balance”, and is well accepted by ecologists.

This naïve conception of “balance” limits the types of equilibrium that are deemed possible or “natural”.

The historical message seems clear: if balance doesn't mean constant numbers, it must mean only small fluctuations in density; if it doesn't mean just small fluctuations it must mean the persistence of a metapopulation. In fact, there must be some kind of balance, we just have to figure out what it is. But, on the other hand, there are certain things that the “balance of nature” concept cannot imply, even when such things are predicted by a more formal definition, mathematical equilibrium. That is, balance of nature, with respect to population number, does not imply extinctions or unpredictability.

It seems that many ecologists still believe that nature is a beneficent force, and that the universe is inherently predictable. I conclude that the "balance of nature" metaphor is a shorthand for the paradigm expressing this worldview. More interestingly, this analysis suggests that metaphors may sometimes play a fundamental role in the development of a scientific discipline, and that historical and cultural concepts may define scientific paradigms.

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