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The "Balance of Nature" Metaphor and Equilibrium in Population Ecology

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Abstract. I claim that the "balance of nature" metaphor is shorthand for a paradigmatic view of nature as a beneficent force. I trace the historical origins of this concept and demonstrate that it operates today in the discipline of population ecology. Although it might be suspected that this metaphor is a pre-theoretic description of the more precisely defined notion of equilibrium, I demonstrate that "balance of nature" has constricted the meaning of mathematical equilibrium in population ecology. As well as influencing the meaning of equilibrium, the metaphor has also loaded the mathematical term with values. Environmentalists and critics use this conflation of meaning and value to their advantage. This interplay between the "balance of nature" and equilibrium fits an interactionist interpretation of the role of metaphor in science. However, it seems the interaction is asymmetric, and the "balance of nature" metaphor has had a larger influence on mathematical equilibrium than vice versa. This disproportionate influence suggests that the metaphor was and continues to be a constitutive part of ecological theories.

Key words: ecology, equilibrium, language, metaphor, science

Introduction

The "balance of nature" metaphor has influenced the development and continued practice of ecology. This metaphor has been used to invoke ideas such as a divinely determined stability, orderliness and predictability in natural systems. The original religious and cultural origins of the metaphor infuse its meaning today, and a related concept "equilibrium". Kingsland (1985) has identified an "equilibrium" paradigm in population ecology, which she characterizes as favouring ahistorical over historical explanations. Ecologists may have adopted this view (e.g. Hastings et al. 1993; Pimm 1991); most historical analyses and contemporary opinion pieces in ecology contrast "equilibrium" and "nonequilibrium" views, particularly in the context of density-dependent vs. density-independent debates. However, careful examination reveals that the "balance" metaphor is a more accurate description of the views of some ecologists identified as belonging to the "equilibrium" camp. Furthermore, most insight into the influence of this metaphor is obtained by examining the conflated uses of "mathematical equilibrium" and "balance of nature" in the ecological literature.

The use of metaphor is a ubiquitous part of the scientific process. It has been claimed that metaphors in science are either pedagogical or pre-theoretical. 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. We may 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, these authors that metaphor is not a substitute for more precise theoretical statements, and claim that as a science or theory matures, its metaphors will be expressed in formal language that subsequently enables predictions (e.g. Boyd 1993).

In other work, it has been claimed that metaphorical language has a fundamental influence on our thought processes. Black (1962) claimed that the use of metaphor is an interactive process in which one subject is projected on another and the two are associated. Black suggests that the two subjects influence then each other, and each one becomes "a lens for seeing the other". Lakeoff and Johnson (1980) claim that all language is metaphorical, and that certain fundamental metaphors constrain the ways in which we can think. That is, metaphors can shape the way we view every aspect of our experience.

These broader interpretations are opposed to the carefully restricted role which metaphor is often assigned to in science. Indeed, it seems quite likely that some metaphors have a larger impact on science than suggested by some authors. Klamer and Leonard (1994) discuss broad-scale theory-constitutive metaphors that frame our way of thinking (as opposed to pre-theoretic metaphors, which are eventually eclipsed by non-metaphorical theory). These conceptual schemes, because of their foundational nature, will tend to frame and influence the whole development of analysis in the new domain. By this definition, theory-constitutive metaphors seem analogous to the scientific paradigms described by Kuhn. They may differ, however, in that such metaphors can be drawn from non-scientific realms. Further, depending on one's interpretation of metaphorical function, these metaphors may simultaneously carry cultural and historical messages.

In population ecology, it might be suspected that the "balance of nature" concept operated as a precursor of the more precisely defined notion of equilibrium. I will demonstrate that there is a dissonance between the meaning of "equilibrium" in mathematical population ecology and the ideas embodied in the metaphor "balance of nature." Further, I will show that in some ecological literature, texts, and critical commentary, the original definition of mathematical equilibrium has been conflated with older ideas about the balance of nature, and imbued with value judgements associated with this concept. Indeed, some critics of the "equilibrium" paradigm in ecology, are much better classified as critics of the "balance of nature" paradigm. These interactions suggest that the metaphor is much more than an imprecise precursor of the theoretical concept of mathematical equilibrium. I conclude that the "balance of nature" metaphor operates in a broad-scale theory-constitutive (Klamer and Leonard 1994) or paradigmatic sense in ecology (Kuhn 1979).

Historical background

The idea that there is balance in nature is part of most world views (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). This interpretation of natural relations is particularly interesting when it refers to interactions that might not be immediately associated with benevolence and balance. 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 in the face of adversity 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 Paley 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 of Species* (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).

Forbes, an influential founding member of the new science of ecology, whole-heartedly embraced the balance of nature concept. 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).

The ancient history of the "balance of nature" metaphor is by no means a proof that it is not operating in a pre-theoretic manner. Indeed, Egerton calls it the first "theory" of ecology (Egerton 1973). 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. As well, the metaphor is not value-neutral: it implies that nature is orderly and beneficent, perhaps in the same way that the, now absent, divine presence had been similarly benign.

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. 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.

Ecology textbooks refer to the ubiquity of balance (Begon et al. 1986). Yet they at the same time discuss the problems of irregularly fluctuating pest species, and lament species extinctions and the destruction of whole ecosystems. 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). We can roughly divide the claims about "balance" into at least three categories: (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, where the removal of one species could cause the collapse of the whole (an associated claim is that communities form a single biological entity and have a characteristic species composition).

The claim about the number of individuals in a population is one of the easiest to understand and to test. It certainly seems the least fraught with political and ethical meanings (e.g. contrasted with the claim regarding “a delicate balance” of ecological relationships and recent debates about biodiversity). It is here, if anywhere, that one should expect to find a modern, non-metaphoric ecological theory, for which the “balance of nature” was a simple verbal approximation.

Beliefs about the balance of population numbers have undergone an historical progression. Although early commentators described population numbers as constant, later ecologists sought to equate observations of variable population size with the “balance of nature”. The earliest idea about populations 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). That is, the natural condition was for population numbers to be constant, while observed deviations were the result of some extraordinary, supernatural event.

After Darwin, population numbers were still claimed to be balanced, although the divine no longer figured in these explanations, instead nature struck a balance. Ecologist Stephen Forbes (1887) supported a claim that the balance of nature maintained population numbers at constant levels,

> 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 . . . .

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 event, the claim that there are more or less constant numbers of individuals in a population was clearly false, even in Forbes’ experience. Scientists expressed doubts about the balance of species numbers from an early date. 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).

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).

His data showed large yearly persisted fluctuations in mammal species across the globe.

Nevertheless, the idea that population numbers were in some way balanced. Howard and Fisk (1911) analyzed populations of gypsy moth and brown fall moth, species noted for their large oscillations in population density, 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 the position of Howard and Fisk 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.

It was also commonly believed that predators would help achieve this regulation of population number. The balance of population number was achieved through a "balance" of predation and reproduction (Packard 1874). Leopold blamed the high density and subsequent population crash of the mule deer on the Kaibab plateau on the fact that the mountain lion, then believed to be a danger to domestic livestock, had been reduced to low levels (Leopold 1943). In this interpretation, an essentially negative relationship (predation), is depicted as having a beneficial effect on the prey, because it promotes a "balanced" population size, where balance (i.e. lack of large fluctuations and little possibility of extinction) is the desired state.

Population equilibrium of predator-prey systems

Simple predator-prey and competition models developed in the 1920s were used to explain, and less commonly, predict, population dynamics of ecological systems. In its early development, mathematical ecology used concepts from physical chemistry. Beginning in 1873, Willard Gibbs published papers on thermodynamics which demonstrated that it was possible the extend equations which described the thermal and mechanical properties of unitary bodies, so that they could be applied to complex systems like chemical solutions. Using these equations, chemical reactions could be were explained by the approach of the system to equilibrium conditions, where the rate of combination and separation of the reactants was exactly balanced.

Volterra and Lotka, two early theorists, used differential equations similar to those used in physical chemistry and analysed the behaviour of these models at equilibrium, in order to make predictions about predator-prey systems. It is doubtful that Lotka and Volterra used an equilibrium approach because they were 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 Poincare), 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. However, the meaning of equilibrium in this context is clear: it is that state where the net rate of change in population density is zero.

In *Elements of Physical Biology*, Lotka also makes clear that some equilibria are stable and others not: "the equilibria in nature, involving countless species, are of course much more complicated in character, but the general principle is the same; and we must expect that in general a variety of different equilibrium are possible, some unstable and some stable" (Lotka 1925). He gives the example of a perfectly screened house, which may be kept free of flies. The fly-free house is in a state of equilibrium, albeit an unstable state. If a few flies make their way through the screen, they will breed and establish a population that will attain some steady number, the stable equilibrium, which depends on the food available and the efforts taken to exterminate the flies. Lotka also discusses the case for which a negative or zero equilibrium density is predicted and notes that it corresponds to the case of species extinction. He gives a relatively sophisticated discussion of the idea that even though a predicted equilibrium is stable, it may still take a very long time for a population to reach that state, and also notes that there may be more than one equilibrium in a system.

The initial, and very simple, models of predator and prey populations that Lotka and Volterra developed predicted sustained oscillations of predators and prey about given population densities, the magnitude of which were determined by the initial conditions of the system. The equilibria for these models were neutrally stable. That is, for any given starting population density of predator and prey, an oscillation around the equilibrium point would occur with no net movement towards or away from the equilibrium densities. Lotka sought to justify this prediction in the words of Hebert Spencer:

> Every species of plant and animal is perpetually undergoing a rhythmical variation in number-now from abundance of food and absence of enemies

> rising above its average, and then by a consequent scarcity of food and abundance of enemies begin depressed below its average ... amid these oscillations produced by their conflict lies that average number of the species at which its expansive tendency is in equilibrium with surrounding repressive tendencies. (Spencer (1882) quoted in (Lotka 1925)).

However, Lotka seems unaffected by the positive values that Spencer attributes to the idea of equilibrium. In his discussion of the predator-prey equations, he notes that although the equations predict oscillations of the predator-prey and no extermination of the prey by the predator, it is nonetheless true that the predator could reduce the prey to very low levels, which could lead to extinction by another one of a myriad of factors, which were, of necessity, not included in the model (Lotka 1925).

Volterra was equally sensitive to the meaning of the various model predictions, and concerned about their realism (Gasca 1996). 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. In disspative systems, individuals of the same species would affect one another, and damped oscillations to a stable equilibrium would ensue. Volterra claimed that "conservative" systems were ideal types, like a frictionless pendulum, and were probably not found in nature (Scudo 1971; Volterra 1926).

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. Nicholson and Bailey, in 1933, developed models of insect populations which had a discrete time-step of one generation. These models predicted not only stable oscillations of predator and prey, but also unstable oscillations that led to the extinction of predator and prey. However, as we shall see, Nicholson and Bailey did not give their readers a careful, or even unbiased, explanation of the meaning of the equilibrium predictions of their model.

The conflation of the meaning of "balance of nature" and mathematical equilibrium

Pimm (1991) asserts that today, ecologists equate the idea of "balance of nature" with "mathematical equilibrium". Therefore, it could be claimed that the "balance of nature" metaphor has now been more precisely defined as the theory that population densities are determined by 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.

In any event, it may seem that I have unnecessarily complicated the issue. Surely there is no confusion about “equilibrium”, with its latin root, *libra*. The word has been used for centuries as a synonym for balance. Deutsch claims that equilibrium is one of the earliest models we have used to order our thoughts, where the metaphor is “the balance, the pair of scales which yields the concept of stable equilibrium” (Deutsch 1951). However, I am not concerned about everyday metaphors of balance, but rather, a scientific concept one of whose possible expressions is a balance. Mathematical equilibrium is a mode of analysis, a research tool, and one way of examining complex phenomena. Early theoreticians discussed some of the possible interpretations of their work with this definition in mind. There is no necessary reason that a given predator-prey interaction will lead to a stable equilibrium; a population density of zero is often no less a stable equilibrium state than some positive constant; and, as originally pointed out by Lotka, very large oscillations in population density could lead to extinctions in a natural system, even though persistence is predicted by the model.

A few examples will show that it is very unlikely that less mathematically sophisticated ecologists really mean “mathematical equilibrium” when they refer to either the “balance of nature” or “equilibrium” in a population ecology context. Ecologists are either unaware of the mathematical models of predator-prey dynamics, in which case it is nonsensical to claim they are in fact referring to mathematical equilibrium of the kind described, or they are aware of the models, but have only understood them as predicting stable, positive and globally attracting equilibrium densities.

Let us take, as an example, the decision to introduce of wolves onto Isle Royale (see Botkin (1990) for an account). In the 1940’s the moose on the island were outstripping their food supply, the park personnel feared a population crash was imminent. They reasoned that moose populations were too high because there were no natural predators on the island, and decided to introduce wolves in order to restore a balance. Clearly, these ecologists thought that the interaction between moose and predators would create a lower moose density. But equally clearly, the park managers did not imagine that wolves would drive the moose population to extinction, nor was it likely that they imagined a very large amplitude oscillation of wolves and moose would occur; after all, the moose were the tourist attraction they were trying to preserve. The equilibrium that the park managers wanted to create was of a very specific kind. Why did they imagine the wolf introduction would create such a balance?

One might answer it was because ecological theory predicted such an outcome. The Lotka-Volterra predator-prey equations do in fact predict that the outcome of a predator-prey interaction may be to, on average, reduce the prey population to a level that might not outstrip the food supply. However, these equations do not necessarily make this prediction. Even the very simple Lotka-volterra equations contain the possible prediction that the sustained oscillations in predator-prey densities would be so large that the predator and prey would go extinct. Certainly, large amplitude oscillations would not be good for the tourist trade, even if extinctions did not occur. Of course, it would probably be more appropriate to model the moose-wolf interaction using a Nicholson-Bailey model with discrete time steps; after all, each species only reproduces once a year. The Nicholson-Bailey equations can predict an unstable equilibrium in which population oscillations increase until predator and prey become extinct. Apparently, since the re-introduction proceeded, the park managers did not consider these to be likely outcomes. Most likely, the park managers were relying on the old "balance of nature" view that predator-prey interactions create more or less constant population densities, and were unaware of the predator-prey model predictions.

When ecologists are aware of the models, it is clear that meaning of "mathematical equilibrium" and "balance of nature" are often conflated. One of the earliest confusions can be attributed to Nicholson. He went to great lengths to answer Elton's assertion the balance of nature does not exist. He claimed that both the ability of a population to weather climatic variation, and the density-dependent nature of predator-prey interactions are expressions of the balance of nature and states that "animal populations must exist in a state of balance, otherwise they are inexplicable" (1933). When he found, however, that his population model of parasite-prey interactions (constructed with Bailey) predicted increasing oscillations in population size, which eventually led to extinction, he claimed that "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, unstable oscillations and extinctions were not characteristic of the balance of nature, and not just any old mathematical equilibrium will do when one refers to "balance".

In their influential text, Allee et al. (1949) give several definitions of equilibrium, all explicitly equated with balance. They also mention the work of Lotka and Volterra, and note that Lotka's work is "becoming more influential as it is slowly disseminated". Slowly indeed, this was written 23 years after its original publication! Equilibrium is defined as “a mean numerical stability, i.e. the average size held by a population over a considerable time,” where “oscillation and/or fluctuation is at a minimum”. Oscillations in population density are discussed under a separate heading and there is no mention of the distinction between stable and unstable equilibrium. Extinction is again in a different section. Clearly, for these authors equilibrium means only a stable, globally attracting equilibrium, with positive population density. It seems likely that the ability of ecologists to understand the population models and the techniques used to derive predictions was severely limited, and consequently, they fell back on older better established concept of “balance”.

Modern definitions of population equilibrium similarly restrict the meaning of equilibrium, although less stringently. In their text, Begon et al. claim that:

> 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).

Even today, one could make an argument that other ecological problems, such as the conservation of wildlife populations, rely on a definition of population equilibrium that does not refer to range of predictions available from a thoughtful interpretation of predator-prey models. Instead, these approaches are predicated on the existence of a stable, globally attracting equilibrium with positive population density. For example, the idea of maximum sustainable yield relies on the assumption that the harvested population is approaching some stable, positive equilibrium density.

It is generally acknowledged that early ecologists were not very sophisticated mathematically. Perhaps it is unrealistic, even today, to expect empirical ecologists to know the esoteric details of the Lotka-Volterra and Nicholson-Bailey models. It is possible to translate these predator prey models and their predictions into English. However, the current use of the term “equilibrium” in the ecological literature makes it clear that in the movement from mathematical model to ecological prediction there has been some confusion. Mathematical equilibriums are not necessary stable; as even my copy of the OED claims, they may also be unstable, neutrally stable, or imply oscillations or extinctions.

Bradie (1999) interprets Lewontin (1963) as suggesting that in the application of a model to the real world some kind of metaphorical identification is necessary. That is, metaphors map a formal mathematical model onto an empirical system. Lewontin’s concern about the potential distortion caused by such application of metaphor seems justified in this case. The “equilibrium" predictions of early models were made understandable to relatively non-mathematical ecologists through the use "balance of nature" metaphor. However, this identification hasn't served mathematical population ecology very well. The concept of "equilibrium" has been narrowly restricted to stable, globally attracting equilibrium, with positive population densities.

Conflation of the value of "balance of nature" and mathematical equilibrium

In addition to influencing the meaning of equilibrium in a population ecology context, the "balance of nature" has also infused the term with cultural values. We can get a hint of this from Nicholson and Bailey. They claimed that extinction was an unlikely outcome of an interaction between predator and prey (1935). However, population extinctions were a known outcome of predator-prey interactions at this time. Although a population extinction is a possible stable state in their model, it does not cohere well with the benevolent interaction of the "balance of nature", and the role that predators were thought to have in maintaining this balance.

This positive connotation of equilibrium continues today. Some current policy equates a stable, positive population equilibrium with the balance of nature, and further identifies the establishment of such equilibrium as a desirable goal. For example, The US Fish & Wildlife Service claims that species extinctions, invasive species (i.e. populations growing exponentially), the loss of natural predators and subsequent large amplitude cycles in prey populations, all threaten the balance of nature. The idea that equilibrium was a good is much less subtle in some works. The equilibrium that is established between interacting species is "somewhat beneficial to both predator and prey" (Allee et al. 1949) and in the case of harmful insects, the restoration of the "natural order" is most beneficial to man as well. More recently, environmentalists often evoke similar images about the role of predators, and appropriate population densities.

In fact, this positive value of equilibrium, and the beneficial relationship between predator and prey is sometimes extended far beyond the ecological realm. Allee et al. (1949) tell us that the "survival of populations increases with the degree to which they harmoniously adjust themselves to each other and their environmental. This principle is basic to the balance of nature ... and is the foundation for all sociology", and will ultimately "contribute to the evolution of human wisdom". Spencer clearly equated equilibrium with a positive end, in fact one that entailed the "greatest perfection and the most complete happiness" (Spencer 1882). We can find similar wide-ranging claims in other fields. Russett suggests that in the in the social sciences "equilibrium" is most often used to convey a feeling of harmony or accommodation among groups in a given situation (Russett 1966).

While ecologists may equate equilibrium with a view that nature strikes a beneficent balance, this is not a necessary connotation of either the word "balance" or "equilibrium". Depending on context, equilibrium can have a positive, negative or even neutral implication. One can see this by comparing the following phrases: my tea had reached equilibrium with the room temperature, he lost his equilibrium, and the moose population equilibrium was restored. I am mildly dismayed about my cold tea, worried about the poor fellow who fell off the curb, and happy that the moose are doing so well (rather than being dismayed by their extinction).

On the other hand, some critics give equilibrium a negative connotation. Opponents, and occasionally environmental proponents, speak about equilibrium predictions as though a divinely-ordered, benevolent natural world is somehow written into $dN/dt = 0$. It is consequently claimed that the entire enterprise of theoretical ecology is suspect because it relies on this fallacious view of nature.

Botkin (1990) gives us one of the more obvious examples of this type of argument. He advances the idea that the original, divinely ordered concept of the "balance of nature" implied that the natural and good condition of ecological systems is static, or at the very least, constant. He discusses ecological theories in a fairly detailed way, distinguishing between stable and unstable equilibriums. He suggests that when he was doing work on the Isle Royale in the 1970s it was "generally accepted that animal populations in undisturbed wilderness were constant over time" (an astonishing claim in itself, it has been known since the 1930s that natural populations can experience large fluctuations in density). However, he claims that the data do not support the theory that "populations achieve a constant abundance or undergo exacting predator-prey oscillations". Botkin's use of "constant" and "constancy" are not accidental. He wishes us to confound the view of a divinely-ordered and static "balance of nature" with the idea of the population equilibrium predicted by the Lotka-Volterra models and other similar models. Then in a sleight of hand, we find that the predictions of these theories are not supported by natural systems, because while "predators and prey can greatly reduce the abundance of the prey or host, there is little evidence that the result is a constancy of nature, a balance in the classical sense" (Botkin 1990). The evidence for or against these models is of little importance, Botkin does not trouble us with much data on the question. His main efforts are expended in demonstrating that nature itself is not constant. He goes on to inform us at great length that the climate, the weather, etc are constantly changing, and so models which assume constant conditions are necessarily doomed to failure.

Clearly, by discounting the older "balance of Nature" view then connecting the metaphor with mathematical equilibrium, which, in all fairness, many ecologists seem to have done, Botkin wishes to discredit a methodological approach to modelling populations. This attack, and similar critiques, has been somewhat successful because of the earlier conflation of both the meaning and value of "equilibrium" and "balance of nature". However, the existence of a population equilibrium density in nature does not imply that population numbers will be constant, or in precise oscillations of predator-prey density. As Lotka discussed, the equilibrium density is not necessarily stable, or static. As well, although mathematical tractability is increased by assuming constant conditions, the use of this approach does not imply that mathematical ecologists believe that nature is constant. Even theoreticians are not so naïve that they believe that weather never changes; analysis at equilibrium conditions is simply a technique for making predictions about the modelled system. From the very beginning, theoretical ecologists have acknowledged these assumptions, and expended their efforts in relaxing them. Nor is it true that any ecologist who has dabbled in equilibrium solutions is uninterested in non-equilibrium behaviour. In fact, equilibrium solutions are used to provide conjectures about the effects of disturbance and environmental variation.

The negative or positive values associated with "mathematical equilibrium" in different contexts can be attributed to connection to the "balance of nature" metaphor. It is certainly not true that all equilibrium solutions map onto a bucolic view of nature. Extinction can be a globally attracting equilibrium, but not many would equate it with the "balance of nature". Neither is it true that "equilibrium" modelling approaches necessarily entail a static and divinely ordered view of nature. The associated value lies in the interpretation of the approach, not the method itself.

Conclusion

The "balance of nature" has operated and still operates as a foundational metaphor in ecology. However, it is unlikely that the metaphor was merely a pre-theoretic version of the idea of "mathematical equilibrium" in population ecology. At least with respect to predator-prey systems, the "balance of nature" metaphor and the more precise definition of equilibrium interact, and have always done so in ecology.

The "balance of nature" metaphor was used to translate the idea of mathematical equilibrium for less mathematically astute ecologists. In the application of this metaphor, some characteristics of mathematical equilibrium were suppressed; ecologists have tended to reject or ignore those types of mathematical equilibrium that don't cohere well with the "balance of nature" metaphor, such as population extinctions, or extremely large oscillations in density. A stable equilibrium density, on the other hand, does cohere well with the notion of balance, and is well accepted by ecologists. That is, equilibrium, with respect to population number, does not imply extinctions or variability. In turn, the idea that the "balance of nature" establishes a constant population size has been replaced by the idea that populations will approach a stable equilibrium of the kind described by simple population models. This transfer of meaning between the metaphor and the more precise mathematical term seems to fit in well with the interaction view of the role of metaphor (Black 1962). However, the relationship has been a little one-sided; the meaning of equilibrium, in a mathematical context, has been very much reduced by the influence of the metaphor, and it is probably fair to say that the understanding of the theory has been impeded by its association with the metaphor.

In addition, through its connection with the "balance of nature" metaphor, the originally value-neutral concept of "mathematical equilibrium" has acquired both positive and negative connotations. A stable population equilibrium is a desirable and natural state (e.g. one that conservation or management efforts should be directed towards). Furthermore, this desirable state can be achieved by a harmonious interaction of predator and prey. On the other hand, critics of the "equilibrium" approach would have us believe that this type of mathematical modelling is neither more nor less than the outdated belief that nature is constant and deterministic, and consequently, should be shunned. Thus the metaphor has changed both the meaning and the values associated with the theoretical term.

This study suggests that, at least in population ecology, the balance of nature metaphor has played, and continues to play a fundamental role. The interpretation of theories has been altered through its influence, research programs condemned or condoned, and conservation or management strategies devised. Regardless of how one regards the strength of its influence, it is clearly not correct to claim that this metaphor was merely an early verbal description of a later theoretical development. Given its ubiquitous influence, it seems likely that the best description of how this metaphor functions in ecology is as a paradigmatic statement.

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