The Lotka-Volterra model and the balance of nature in conservation

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This paper examines the enduring 'balance of nature' concept, arguing that it persists in contemporary ecology because of unexamined philosophical assumptions rather than empirical support. Beginning with its roots in ancient Aristotelian philosophy and tracing its survival through the Darwinian revolution, my analysis shows how the Lotka–Volterra model assumes an equilibrium ideal. I argue that this assumption should be reframed as a testable scientific hypothesis rather than treated as background truth. Conservation priorities could then shift. Instead of aiming to maintain an imagined equilibrium, efforts can focus more on reducing human-driven ecological disturbance. The paper concludes by proposing a revised framing for ecology and conservation efforts, one that recognises the central role of anthropogenic impacts.

1. Introduction

The idea that nature is balanced arose implicitly during early Western philosophy, and survived the Darwinian revolution. The contemporary form of this idea can be seen in the Lotka-Volterra model which posits an equilibrium state whereby the predator-prey balance of a population is kept. However the balance of nature concept is contingent upon an a-priori claim; and we can see this claim as an implicit assumption that ecologists have failed to question. The problem is that if we search for empirical evidence supporting the claim that nature is balanced, then the conclusion is far from clear. The result of questioning this fundamental assumption of ecology is the very aim of research and by extension conservation efforts could shift. I will begin this essay by briefly placing the balance of nature concept in its historical context. I will then explicate this concept, making the specific claim underlying the concept clear. I will then move on to contemporary mathematical ecology, analysing how the Lotka-Volterra model implicitly assumes that nature is in equilibrium; that is, it is balanced. I will argue that this claim should be seen as a scientific hypothesis that needs empirical evidence for support, rather than an assumption that be accepted on faith. From this I will suggest an alternative perspective whereby conservation efforts can shift from maintaining equilibrium in the ecosystem, to reducing human impact on the ecosystem.

2. Balance of nature: historical context and contemporary form

Western philosophy has traditionally held that nature is essentially fixed and change is a sign of imperfection. Aristotle's conception of nature was such that each species, *eidos,* had a purpose towards which it grew; and "this progressive organisation does not cease till there is achieved a true final term, a telos, a completed, perfected end."[1] The genesis of the balance of nature concept can thus be found in antiquity, however the concept had only emerged implicitly.[2] During the seventeenth century "the idea became a functional assumption, but within a theological rather than ecological context;"[3] and in William Paley's 1802 work *Natural Theology,* it was "advocated that God must be ensuring a

1 John Dewey, *The Influence of Darwin on Philosophy and Other Essays* (New York: Henry Holt and Company, 1910), pg 4.
2 Frank Egerton, 1973, 'Changing Concepts of the Balance of Nature,' *The Quarterly Review of Biology,* vol. 48, no. 2, pg 322.
3 Ibid.

balance of nature."[4] Whilst a student at Cambridge, Darwin read Paley's work;[5] and whilst Darwin marked the beginning of an intellectual revolution, he failed to challenge the assumption that nature is balanced. He subsequently referred to the concept in his own work, and in *Origin of Species* Darwin wrote the following:

> Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so *nicely balanced*, that the face of nature remains uniform for long periods of time.[6]

Despite Darwin setting out his theory of natural selection and challenging orthodox thought, it is still assumed and furthermore explicitly stated that nature is 'nicely balanced.' However when we refer to the 'balance of nature,' what exactly do we mean? That itself is one of the difficulties because "there have been few attempts"[7] to agree upon a specific definition. This problem being "the consequence of the concept having been a background assumption rather than a hypothesis or theory."[8] Egerton, who has documented the history of the idea, notes that "any balance-of-nature concept will assume an approximate stability in the populations of species."[9] The concept has been roughly defined in the following terms:

> Biologists...feel that the organisms in a community are harmoniously adjusted to one another so that a state of dynamic equilibrium exists. In this equilibrium the numbers of the individuals of each species in the community remain relatively constant, and significant changes in numbers occur only when something upsets the natural "balance."[10]

In other words, the number of species and individuals in any given ecosystem should remain reasonably constant, and large fluctuations in population size are somehow 'unnatural.' Cooper has explicated the balance of nature argument which begins with the claim that "the relative constancy of population sizes...implies that populations are regulated."[11] It is assumed that "there is a kind of stability and orderliness to the biological world"[12] that is protected against the vicissitudes of nature. Cuddington has made this explicit by noting that underlying the balance of nature argument are two related claims:

> The claim that natural populations have...constant numbers or individuals...the claim that natural systems have a...constant number of species.[13]

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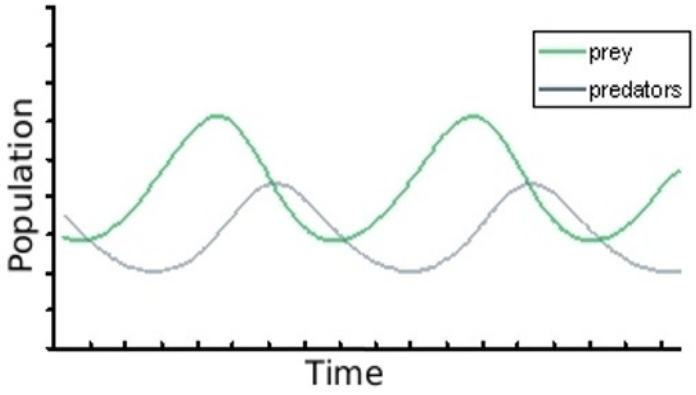
4 Dennis E. Jelinski, 2005, 'There Is No Mother Nature: There Is No Balance of Nature: Culture, Ecology and Conservation,' *Human Ecology*, vol. 33, no. 2, pg 277.
5 Ibid., pg 277.
6 John Kricher, *The Balance of Nature: Ecology's Enduring Myth* (New Jersey, United States: Princeton University Press, 2009) pg 65.
7 Frank Egerton, 1973, 'Changing Concepts of the Balance of Nature,' *Quarterly Review of Biology*, vol. 48, no. 2, pg 324.
8 Ibid., pg 324.
9 Ibid., pg 324.
10 C. Birch and P. R. Ehrlich, 1967, 'The "Balance of Nature" and "Population Control," *The American Naturalist*, vol. 101, no. 918, pg 97.
11 Gregory Cooper, 2001, 'Must There Be a Balance of Nature?,' *Biology and Philosophy*, vol. 16, no. 4, pg 483.
12 Ibid., pg 483.
13 Kim Cuddington, 2001, 'The "Balance of Nature" Metaphor and Equilibrium in Population Ecology,' *Biology and Philosophy*, vol. 16, no. 4, pg 466.

This results in a “delicate balance of relationships, where the removal of one species could cause the collapse of the whole.”[14] The key term to note is constant; and when we speak of the 'balance of nature' we are really speaking of the claim that there is a constant number of individuals and species in any given ecosystem. Once pointed out, it may seem obvious that this is an empirical question that can be settled through empirical evidence. However “there has been a significant effort to argue...primarily on conceptual grounds;”[15] and in ecology, this claim has become an implicit assumption. That is, the theory underpinning the science of ecology assumes that the balance of nature does exist; and “Pimm...asserts that today, ecologists equate the idea of “balance of nature” with “mathematical equilibrium.”[16] This can be seen most clearly in the Lotka-Volterra model.

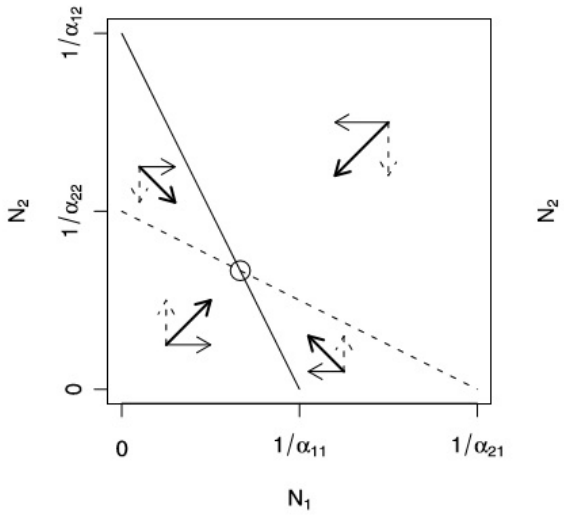
This model describes how the competition between predator and prey affects the growth of each. It explicitly states that when a population reaches a state of equilibrium, then this population is experiencing a stable coexistence. The word 'equilibrium' comes from the Latin 'aequilibris' and can be loosely understood as meaning “an even balance.”[17] Thus, according to the model, when an even balance in population size is reached, then stable coexistence is assured. The model predicts oscillations in population size, but balance is achieved when there is zero net growth such that over time there is no dramatic change in overall population numbers. In other words, minimal overall change means the species are in equilibrium. This state of equilibrium, this state of balance, is then equated with health. As Kim Cuddington makes clear, “for any given starting population...an oscillation around the equilibrium point would occur with no net movement towards or away from the equilibrium densities.”[18] We can see this in the graph below where the population of either species is changing, however this change happens around a fixed equilibrium such that the population is in a state of dynamic equilibrium:



The Lotka-Volterra Equation

14 Kim Cuddington, 2001, 'The “Balance of Nature” Metaphor and Equilibrium in Population Ecology,' *Biology and Philosophy*, vol. 16, no. 4, pg 466.
15 Gregory Cooper, 2001, 'Must There Be a Balance of Nature?,' *Biology and Philosophy*, vol. 16, no. 4, pg 482.
16 Ibid., pg 470.
17 Douglas Harper. “*Equilibrium*.” Online Etymology Dictionary: Accessed October 29, 2017. url: etymonline.com/word/equilibrium
18 Kim Cuddington, 2001, 'The “Balance of Nature” Metaphor and Equilibrium in Population Ecology,' *Biology and Philosophy*, vol. 16, no. 4, pg 469.

The graph below[19] represents the equilibrium point where the two species reach stable coexistence. Crucially, this "equilibrium is...a point at which the growth rates of all populations are zero."[20] As we can see, any dramatic change in either species population – N1 or N2 – would create disequilibrium.



(a) Stable coexistence

The assumptions of the model are clear. An equilibrium population size does exist, and furthermore peaceful coexistence depends upon reaching this equilibrium. However this is an implicit assumption that the Lotka-Volterra model has made, and this assumption is clearly due to the history of the balance of nature concept rather than empirical evidence. Lotka did realise this assumption and "sought to justify"[21] his position. However he did so by relying on the words of Herbert Spencer who failed to question tradition. It was again assumed that "every species of plant and animal is perpetually undergoing a rhythmical variation,"[22] and within these variations "lies that average number of the species at which its expansive tendency is in *equilibrium*"[23] (italics mine).

Despite the advance of ecology as a science, the balance of nature concept clearly survived both the Darwinian and mathematical revolutions, and continues to be "interpreted as persistence with limited change in population number."[24] McCann is clear about the problem, writing that ecological theory has traditionally relied "on the assumption that a system is stable if, and only if, it is governed by stable equilibrium dynamics."[25] However McCann advises that "these are strong assumptions with no a priori justification,"[26] and as we have seen this assumption has a long history and is rarely treated as a working hypothesis or theory. However once we explicate the vague 'balance of nature' concept and

19 M. H. H. Stevens, *A Primer of Ecology with R* (New York: Springer, 2009) pg 147.
20 Ibid., pg 141.
21 Kim Cuddington, 2001, 'The "Balance of Nature" Metaphor and Equilibrium in Population Ecology,' *Biology and Philosophy*, vol. 16, no. 4, pg 469.
22 Ibid., pg 469.
23 Ibid., pg 470.
24 Ibid., pg 468.
25 Kevin Shear McCann, 2000, 'The diversity–stability debate,' *Nature*, vol. 405, no. 6783, pg 229.
26 Ibid.

re-phrase it to the claim 'there is a constant number of individuals and species in any given ecosystem,' then we can view it is an hypothesis that needs testing. It is true that once evidence is sought, it is not clear what the answers are:

> The degree of constancy in population size that one finds appears to depend a great deal on the kinds of organisms one studies...It is an empirical question, and one that appears to be largely still up in the air.[27]

As Cooper further notes, questions concerning the balance of nature should "be settled by empirical study."[28] It is therefore necessary that the balance of nature assumption is recognised and then treated as a working hypothesis that needs testing, rather than taken on faith or tradition. One may accuse me of arguing that the a-priori has no place in science. I am not saying this. Rather, I am pointing out that the balance of nature concept is treated as an implicit assumption in ecology, and it continues to underpin the theory. This concept should not be taken for granted just because we may intuitively perceive a balance in nature. We may intuitively think that the earth is flat, or the earth is the centre of the universe. However the evidence tells us otherwise, and as J. J. C. Smart advises "theories have to be tested by facts."[29] It may have been reasonable to conceptualise nature as 'balanced' in the past before the scientific revolution and the wider acceptance of secularism as legitimate. However one of the very cornerstones of science is to update theories based upon the evidence. The balance of nature concept needs empirical evidence for support, and if evidence cannot be found, then the assumption should be rejected or mitigated. The concept is the remnants of a picture of reality that has changed dramatically since the times of Aristotle. The problem is that it still lingers in the background of ecological thought, and by extension would also drive conservation efforts. It is not a harmless fiction or metaphor that is used to understand reality. It is an implicit assumption that needs challenging and testing.

3. Paradigm shifts in ecology and the affect on conservation efforts

Once we perceive the balance of nature concept as an hypothesis rather than an assumption to be accepted on faith, then a different set of questions can begin to be asked. We can see this as a paradigm shift within ecology whereby the very aim of research and by extension conservation efforts change. That is, if we reject the balance of nature concept, then what exactly is the aim of our efforts when we protect ecosystems, and what role can ecology play in this? In his study *The Balance of Nature: Ecology's Enduring Myth*, John Kricher offers a solution to the problem by suggesting that biodiversity is the key to ecosystem health.[30] However Kricher fails to question tradition by continuing to equate stability with health, and continuing the very myth that he sets out to destroy. Whilst Kricher begins the study by describing the balance of nature concept as "philosophical

27 Gregory Cooper, 2001, 'Must There Be a Balance of Nature?,' *Biology and Philosophy*, vol. 16, no. 4, pg 484.
28 Ibid., pg 482.
29 J. J. C. Smart, 1999, 'Ruth Anna Putnam and the Fact-Value Distinction,' *Philosophy*, vol. 74, no. 289, pg 432.
30 John Kricher, *The Balance of Nature: Ecology's Enduring Myth* (New Jersey, United States: Princeton University Press, 2009) pg 180.

baggage,"[31] he then reinstates this concept by suggesting that we maintain biodiversity because it promotes ecosystem stability. During the final chapter, Kricher states the following:

> Researchers also assert...that restoring biodiversity to areas of the oceans where it has been impoverished will allow the full recovery of productivity and stability.[32]

In this sentence the true intentions of the author is made clear. Biodiversity should be restored, however the ultimate aim is still, in keeping with tradition, full recovery of ecosystem stability. Kricher admits that "the role of biodiversity in maintaining ecosystem stability is muddled," however the implication of this view is clear. The word 'stable' can be used as a synonym for 'balance.' Therefore when Kricher suggests that biodiversity must be sought in order to maintain ecosystem stability, he is really calling for biodiversity only because it promotes ecosystem balance. Despite also factoring in other measurements of ecosystem health such as productivity, the central problem remains. There is an assumption that ecosystems are inherently stable, that is inherently balanced, and any factor that disturbs this stability is somehow unnatural. Despite Kricher's stated intention, I find it difficult to see in the ultimate conclusion any real challenge to tradition. However the author hints at an alternative perspective when he states where exactly the source of destruction lay:

> There is general agreement among ecologists that anthropogenic activity resulting in loss of habitat is the major cause of the ongoing global decline in biodiversity.[33]

One specific case of apes in Gabon is cited where a fifty percent decrease in the population size occurred over a brief time period. It was concluded that "human hunting pressure associated with increased mechanized logging of the region was a principal cause of the decline."[34] Kricher writes that "human population growth in western equatorial Africa has brought apes to the verge of extinction,"[35] and multiple case studies have documented "the cumulative negative impacts of anthropogenic activities."[36] A recent article in *The Guardian* is more broad and ominous but also clear in its warnings:

> The term Anthropocene...acknowledges that humans are the major cause of the earth's current transformation...the human species is...driving global warming and ecological destruction.[37]

In other words, a large part of ecosystem destruction is done at the hands of the human animal. The pragmatic conclusion to the debate on the aim of conservation efforts would

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31 John Kricher, *The Balance of Nature: Ecology's Enduring Myth* (New Jersey, United States: Princeton University Press, 2009) pg 7.
32 Ibid., pg 184.
33 Ibid., pg 174.
34 Ibid., pg 177.
35 Ibid., pg 177.
36 Ibid., pg 178.
37 Alex Blasdel. "*A reckoning for our species': the philosopher prophet of the Anthropocene*." The Guardian: Accessed October 28, 2017. url: theguardian.com/world/2017/jun/15/timothy-morton-anthropocene-philosopher

be to focus on what can be known and then changed. This can be done by focusing efforts on the human factor in ecological destruction, which is clearly large. An exemplar of this would be plastic in the oceans. Laura Parker of *National Geographic* writes that "scientists know a great deal about the damage to marine life caused by large pieces of plastic,"[38] and it is estimated that "there are 5.25 trillion pieces of plastic debris in the ocean."[39] Both the problem and solution should be clear. There is too much plastic in the ocean, and the amount of plastic that *humans* place into the ocean must be reduced. Peter Ryan, a zoologist at the University of Cape Town, echoes this sentiment by saying that "marine debris, unlike global warming, should be an easy thing to deal with...we have to sort out what to do with our rubbish."[40] Rather than attempt to reintroduce 'balance' into ocean ecosystems, it would be more prudent to work on decreasing the pressure that humans place on the ecosystem. The reason is simple. If the actions of humans have the largest impact on ecosystem health, then mitigating this impact would have the largest benefit. Balance is not restored, and stability is not a goal worth aiming for. Rather, we allow nature to grow and play with freedom, and focus our efforts on what can be known and then changed.

The original question 'what would it mean for Nature to be in balance?' makes the same error that ecology has made. It implicitly assumes that nature is in balance. The main task of the philosopher is then to define this balance. However as Wittgenstein advises, "without philosophy thoughts are, as it were, cloudy and indistinct: its task is to make them clear and give them sharp boundaries."[41] One of the powers of philosophy is to bring to the fore implicit assumptions and make it clear how our convictions and knowledge can rest on contradictory ideas. In this paper I have not directly answered the original question because, as I have argued, the balance of nature concept is problematic and needs challenging. It is the outcome of tradition, not scientific practice, and until sufficient evidence is found to support the concept, then judgement should be withheld.

38 Laura Parker. "*Ocean Trash: 5.25 Trillion Pieces and Counting, but Big Questions Remain*." National Geographic: Accessed October 28, 2017. url: nationalgeographic.com/news/2015/01/ 150109-oceans-plastic-sea-trash-science-marine-debris/

39 Ibid.

40 Ibid.

41 Ludwig Wittgenstein, *Tractatus Logico-Philosophicus* (New York: Routledge, 2001), pg 30 (4.112).

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