

O P I N I O N O P I I O N

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The anarchist's guide to ecological theory. Or, we don't need no stinkin' laws

R. B. O'Hara, Dept of Mathematics and Statistics, P.O. Box 68 (Gustaf Hällströmin katu 2b), FIN-00014 University of Helsinki, Finland (bob.ohara@helsinki.fi).

Several ecologists have recently suggested that ecology has several laws. This conclusion contrasts with the views of some philosophers of science, who have suggested that biology cannot have laws. I argue that the debate has been confused because two very different types of law can be recognised: correlative and causal laws. Once we recognise that there is a difference, the argument against causal laws becomes stronger, and instead I suggest that ecologists should recognise that they can and do produce generalisations that are used to build models – nomological machines – that describe the ecological systems they are studying.

physics – relativity and quantum physics – are not described as laws, but rather as theories and principles (Einstein's theories of relativity, quantum theory, Heisenberg's uncertainty principle). Whilst a full examination of the development of the epistemology of physics is beyond the scope of this paper, it certainly appears that laws have become old-fashioned – at least for physicists. And if physicists feel that they do not need laws, why should anyone else?

There has been a discussion in the ecological literature about whether ecology has any Laws of Nature and what those laws might be (Lawton 1999, Murray 2000, Turchin 2001, Colyvan and Ginzburg 2003). The consensus between the discussants is that there are laws, even if they are not quite sure what these laws are. A similar discussion between philosophers has led to a consensus that biology (let alone ecology) does not have Laws of Nature, at least as they are traditionally understood by philosophers (Beatty 1995, Brandon 1997, Mitchell 1997, 2000, Cooper 1998). Why is there such a difference of opinion, and if (as I will argue) the philosophers are correct, what are these things that have been proposed as ecological laws?

The discussion of ecological laws started from the suggestion that ecology as a science should model itself on physics, and as a part of this imitation, it should develop its own laws of nature (Murray 1992, Colyvan and Ginzburg 2003). The logic behind this seems to rest on the observations that physics is successful, and also that it has Laws of Nature. From these observations it is deduced that it is the laws that make physics successful, and hence that other sciences (in particular ecology) which do not have laws cannot be successful.

Before we examine this inference, it is amusing to observe that the two main successes of twentieth century

What is a Law of Nature?

One problem that has faced those discussing laws of ecology is giving a description of what a Law of Nature is. In part, this appears to be because there are two rather different types of regularity that may be elevated to the status of a law (Waters 1998). The first form of law I will call a correlative law (in preference to the term “distributions” used by Waters). These are observed regularities, for example Rapaport's rule (that diversity increases towards the equator) and are derived as generalisations from a large number of observations. They have a predictive power, e.g. there is a high diversity in Cameroon because it is on the equator, but only a weak form of explanatory power, in the sense that they do not provide a deeper understanding of the processes that lead to the observations (e.g. Rapaport's rule does not say why diversity increases towards the equator). They describe correlations, but the correlations need not be causal: it is clear that it is not the equator itself that causes a higher diversity, but instead there are other factors that cause the higher diversity and are correlated with latitude.

The second type of regularity is what Waters termed a causal law. This is a statement about the mechanisms that give rise to observed regularities. They include

Newton's Laws of Motion and the regularities proposed by Turchin (2001). These are different in nature from correlative laws in that they are intended as descriptions of the way that the universe works, rather than of the regularities that happen to have been found in the universe. They are intended as statements about causation.

When philosophers have defined Laws of Nature, they have typically been thinking of causative laws. They typically declare that a statement needs to overcome two hurdles before it can be considered a Laws of Nature (Salmon 1992, Brandon 1997). Firstly, it has to have a natural necessity – i.e. it has to be true because of the way the world is. This means that it has to have some empirical content: a mathematical theorem is not a Law of Nature because it is true by virtue of logic. Secondly, the law has to be essential scientifically, i.e. it has to be used. So, for example, several authors (e.g. Turchin 2001) have proposed a Malthusian law, that a population in a constant environment will grow exponentially. This lacks essentiality: a population with discrete generation times will not grow exponentially, but geometrically – as Malthus himself observed (Malthus 1798). Additionally, individual-based models of populations have no need of a Malthusian law.

Colyvan and Ginzburg (2003) argued that laws can have exceptions. They used Galileo's law as an example, pointing out that an exception can be found by comparing the accelerations of snowflakes and hailstones. This is problematic, because they do not give any indication about how many exceptions are allowed before a law has to be repealed. How one deals with this depends on whether one's law is a correlative or causal law. Both types of law might have exceptions, but the response to them can be very different.

The classic response to an exception is to argue that not all of the conditions for the law to operate apply, for example the orbit of a planet may be incorrect because of the effect of another planet's gravity (Lakatos 1970). With causal laws, we have to be aware of why they do not operate. Cartwright (1999) has suggested that laws only operate in special conditions, when they are "shielded" from other effects. She suggests that if the shielding is insufficient, then the law is not operating. This solution cannot be satisfactory, as it either means that no laws are acting, or that (as Cartwright proposes), there are several domains of nature, with conflicting laws. The former is unsatisfactory because it means that the universe is random (and then how are the probabilities of events assigned? By laws?), and the latter needs some rules from when each domain is dominant: these would surely be laws too. The problem is that Cartwright, too, is confounding correlative and causal laws: her definition of laws is "descriptions of what regularly happens" (Cartwright 1999, p. 4), i.e. as correlative laws, but she then attacks a "fundamentalist" position which uses a

causal law interpretation of a law (pp. 24–28). Her solution is to make "capacities" fundamental to science. These are innate properties of objects that engender the potential for things to happen. Causal laws are then statements about capacities, rather than statements about what actually happens (Chalmers 1999). Statements about what actually happens can be made by applying the laws to describe the actual situation (below).

Of course, it could also be that a statement intended as a causal law is false, in which case it should no longer be regarded as a law. For example, Colyvan and Ginzburg cite the failure of the law of conservation of kinetic energy. But, this has been supplanted by the law of conservation of energy (which in turn has been supplanted by Einstein's theories of relativity!). Just because a statement was once called a law does not mean that it is a Law of Nature.

Correlative laws are more forgiving of exceptions. Because they are observed regularities, there is no ontological necessity to always be correct. If an exception to a correlative law is found, an explanation for the exception is desirable, but is not necessary – the rule will still be true generally. Indeed, it can be passed off as "the exception that proves the rule", and used to gain a deeper understanding of why the correlative law is the way it is, by using the exception to show the limits to the domain of applicability of the law (Weber 1999).

Different participants in the discussion of ecology have taken different positions on what sort of law it is that they are discussing. Lawton (1999) used "law" in a very wide sense, to include both correlative and causal laws. Colyvan and Ginzburg (2003) also use a wide sense of "law", to include correlative laws. However, Murray (2000) and Turchin (2001) suggest laws that are clearly causal laws, with a much narrower epistemological scope. This is in line with the usage of most philosophers (e.g. in this context Beatty 1995, Brandon 1997). Not being clear about these differences might result in participants in the discussion talking past each other, as when those proposing exclusively causal laws use the writings of those using laws in their wider sense as support. As the recent attempts at propounding laws have been focussed on the narrow sense interpretation, I will also use "laws" to mean causal laws – Laws of Nature, rather than Generalisations from Nature. The status of correlative laws should be less controversial, and the status of any particular law is a matter of empirical investigation.

Biological laws

Why have philosophers of science decided that biology does not have laws? Firstly, it has to be noted that the philosophers are discussing causal laws. Beatty (1995)

suggested that any law of biology (other than those which are really laws of physics or chemistry) are contingent on evolution. For example, the truth of the statement “all insects have six legs” is a matter of evolution, as is the falsity of the statement “all insects have four wings”, because some groups of insects (e.g. the *Diptera* and *Coleoptera*) have, through evolution, changed the functions of their wings. Beatty argues that this contingency means that any law-like biological statement is not universal: it is only ever conditional on the evolutionary process, and is therefore not a law of nature.

Weber (1999) has criticised Beatty’s argument. He used Gause’s principle of competitive exclusion as an example of a law-like statement that is not contingent on evolution, and used it to demonstrate his view that there are ecological laws, but only ones that apply in a small domain. The problem (as Weber admits) is that the domain of applicability cannot be specified. He feels that this is not a problem, because some of the features of the domain can be sketched. I would disagree, because unless one can specify the domain of applicability, Weber’s characterisation that ecological laws exist “if they are construed as universally valid only within that domain, and inapplicable outside of it” is trivially true of any statement: one simply dismisses any counter-example as being outside the domain of applicability.

A similar problem can be seen in Turchin’s (2001) proposal of a Malthusian law (that a population will grow exponentially). Turchin shows that the general form of the law has to be adapted to specific cases: to turn the principle into a law, one has to limit its domain of applicability and then alter the principle to fit the law. So, the “Law” only fits a restricted domain, and has to be adapted to fit the biology before it has any empirical content. In contrast, physical laws have mathematically unique forms (e.g. Newton’s second law is $F = ma$). The other “Laws” that Turchin proposes are even vaguer than his Malthusian Law (which, in its general form, can at least be summarised by a mathematical representation), and this seems typical of the laws that have been proposed (Murray 2000, Berryman 2003). Any law-like statement therefore appears to be either too vague to be tested empirically, or too restricted in scope to act as a good Law of Nature.

Lawless, but not unprincipled

Even if we accept that there are no laws of ecology, this does not mean that the proposed laws are useless for ecology. I would suggest that a more sophisticated epistemology is needed to understand the role of these sorts of statements within ecology. Mitchell (1997) suggests that a pragmatic approach to laws

and other generalisations should be taken. One advance in this direction has come from the work of Cartwright (1999, ch. 6). She looked at research in economics, and observed that economic laws (such as the law of supply) do not act in isolation, but rather as part of a larger system (e.g. the law of supply has to operate along with the law of demand). This seems similar to ecological systems, where it is rare that single factors operate (Beatty 1997), and the process of modelling ecological systems consists of deciding which set of factors are operating. Malthus’ “Law” (for example) provides a general heading for one factor, but there are several ways of using this, and which version is to be used will depend on the precise biology of the system being studied. Similarly, there will be cases where population self-limitation is important, and here the appropriate/favourable form of limitation will be chosen to represent the system being studied (e.g. a logistic growth curve, or a Ricker equation).

Cartwright (1999) has argued that when we try to explain natural phenomena, we do so by building a “nomological machine”. We can think of this as a machine made up of several components which can interact with each other to produce a behaviour which is (hopefully) like that of the natural world which is being modelled. The “Laws” of Turchin are not descriptions of how nature is governed, but rather are descriptions of parts of nomological machines, from which different components can be selected as needed. They are fundamental to the way that ecology is carried out, because much of ecological theory is built on their foundations. For example, any model of population dynamics will have the Malthusian axiom at its heart, even if the precise mathematical formulation can vary. Mitchell (2000) points out that this description of science is closely linked to the ideas of Kuhn (1962) and Lakatos (1970), with ecology as a research paradigm (Kuhn) or programme (Lakatos). The axioms that have been proposed as laws are the fundamental ideas of the research programme (Lakatos’ hard core, or Kuhn’s “rules of the game”). They define the: the problems and puzzles that are investigated. Making them explicit is valuable because it enhances our understanding of the research programme, and allows us to see the strengths and weaknesses of the theoretical framework that has been constructed.

Are we in trouble?

If ecology does not have (causal) laws, does this mean that ecology cannot be a successful science? The evidence from both ecology as well as other sciences, which do not work with laws, suggests that it can. A common criterion for deciding whether a science is successful is whether it

is predictive, i.e. if it can produce theories that can successfully predict behaviours of the real world (Turchin 2001, Colyvan and Ginzburg 2003). Many examples can be found of predictive science from disciplines which do not have laws. One example comes from plant pathology. One way of improving the performance of crops without a heavy use of pesticides is to sow varieties with different resistance genes, creating variety mixtures. The theory behind these was developed during the 1970s (Barrett 1980), and experimental work showed their effectiveness in practice (Wolfe et al. 1981). This led to barley mixtures being sown over large areas (360 000 ha, or 92% of the total area sown) of East Germany, leading to a reduction in powdery mildew infection, and fungicide use (Mundt 2002). The theory was developed from simple models of growth and dispersal, without invoking any Laws of Plant Pathology. Instead, a core of principles were used to develop the models in a seemingly ad hoc manner.

The example of plant pathology is instructive because it is an example of successful population biology where Laws of Nature are not pursued. If plant epidemiologists are able to make successful predictions about the development in pathogen populations, there seems little reason why population biologists cannot do the same. There is therefore no reason why ecologists have to follow epistemological paths set out from philosophers' studies of physics. Rather than looking for Laws of Nature, ecologists should be content to look for broad generalisations, from which nomological machines can be built that will act as models of specific systems. This is the path that ecology is taking anyway, and which is becoming recognised by philosophers of science (Cartwright 1999, Mitchell 2000, Mikkelsen 2003); Cooper (2004) provides a good discussion of the issues involved, with particular reference to ecology. Population biology is well advanced in this regard, with several principles having been suggested (Turchin 2001, Berryman 2003). The pursuit of these generalisations is desirable, because they will bring a cohesion to ecology. However, calling them laws is to give them an epistemological status that they do not deserve. Quite simply, the "Laws" are not strict enough to judge if a species has broken a law; in its defence the species can simply suggest that the law should be re-interpreted.

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References

- Barrett, J. A. 1980. Pathogen evolution in multilines and variety mixtures. – *Z. Pflanzenkrankheiten Pflanzenschutz* 87: 383–396.
- Beatty, J. 1995. The evolutionary contingency thesis. – In: Wolters, G. and Lennox, J. G. (eds), *Concepts, theories and rationality in the biological sciences*. Pittsburgh Univ. Press, pp. 45–81.
- Beatty, J. 1997. Why do biologists argue like they do? – *Philos. Sci.* 64 (Proc.): S402–S443.
- Berryman, A. A. 2003. On principles, laws and theory in population ecology. – *Oikos* 103: 695–701.
- Brandon, R. 1997. Does biology have laws? The experimental evidence. – *Philos. Sci.* 64 (Proc.): S444–S457.
- Cartwright, N. 1999. *The dappled world: a study of the boundaries of science*. – Cambridge Univ. Press.
- Chalmers, A. F. 1999. What is this thing called science?. – Oxford Univ. Press.
- Colyvan, M. and Ginzburg, L. R. 2003. Laws of nature and laws of ecology. – *Oikos* 101: 649–653.
- Cooper, G. 1998. Generalizations in Ecology: a philosophical taxonomy. – *Biol. Philos.* 13: 555–586.
- Cooper, G. J. 2004. *The science of the struggle for existence*. – Cambridge Univ. Press.
- Kuhn, T. S. 1962. *The structure of scientific revolutions*. – Chicago Univ. Press.
- Lakatos, I. 1970. Falsification and the methodology of scientific research programmes. – In: Lakatos, I. and Musgrave, A. (eds), *Criticism and the growth of knowledge*. Cambridge Univ. Press, pp. 91–195.
- Lawton, J. H. 1999. Are there any general laws in ecology? – *Oikos* 84: 177–192.
- Malthus, T. R. 1798. *An essay on the principle of population*, J. Johnson, London, UK.
- Mikkelsen, G. M. 2003. Ecological kinds and ecological laws. – *Philos. Sci.* 70: 1390–1400.
- Mitchell, S. D. 1997. Pragmatic laws. – *Philos. Sci.* (Proc. 64): S468–S479.
- Mitchell, S. D. 2000. Dimensions of scientific law. – *Philos. Sci.* 67: 242–265.
- Mundt, C. C. 2002. Use of multiline cultivars and cultivar mixtures for disease management. – *Annu. Rev. Phytopathol.* 40: 381–410.
- Murray, B. M. Jr. 1992. Research methods in physics and biology. – *Oikos* 64: 594–596.
- Murray, B. M. Jr. 2000. Universal laws and predictive theory in ecology and evolution. – *Oikos* 80: 403–408.
- Salmon, W. C. 1992. Scientific explanation. – In: Salmon, M. H. et al. (eds), *Introduction to the philosophy of science*, pp. 7–41.
- Turchin, P. 2001. Does population ecology have general laws? – *Oikos* 94: 17–26.
- Waters, C. K. 1998. Causal regularities in the biological world of contingent distributions. – *Biol. Philos.* 13: 5–36.
- Weber, M. 1999. The aim and structure of ecological theory. – *Philos. Sci.* 66: 71–93.
- Wolfe, M. S., Barrett, J. A. and Jenkins, J. E. E. 1981. The use of cultivar mixtures for disease control. – In: Jenkyn, J. F. and Plumb, R. T. (eds), *Strategies for the control of cereal disease*, pp. 73–80.

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