Laws in ecology: diverse modes of explanation for a holistic science?

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ABSTRACT

Ecology's reputation as a holistic and soft science is partly due to widespread misconceptions of its nature as well as shortcomings in its methodology. We show how the pursuit of empirical laws of ecology can foster the emergence of a more unified and predictive ecology based on complementary modes of explanation. Numerical analyses of population dynamics have a distinguished pedigree, spatial analyses successfully generate predictive laws for macroecology and physical analyses are tyically pursued by the ecosystem approach. The most characteristically ecological laws, however, are found in biotic analyses within the 'functional trait' paradigm. Holistic credentials for ecology may thus be restored on two bases: its accommodating complementary modes of analysis and explanation, and its having some laws within the least reductionistic mode consistent with its subject matter. These claims, grounded in the aspectual theory of Herman Dooyeweerd, lead to some suggestions for enhancing the versatility and usefulness of ecology – and other sciences – by balancing different research paradigms under a holistic vision.

Keywords: abstraction, biotic, physical, spatial, numerical, [mode], [holistic], paradigm, reductionism

Ecology, as the study of general patterns in the relationship of organisms to their environments, appears to be a holistic science. This notion is no doubt bolstered by its links to an ideology. What English-speakers call *green* is rendered in many other languages as *ecological*, which (also in English) evokes the ethic of conservation and certain kinds of nature-focused worldviews and lifestyles that reject reductionistic explanations and technologies. But all kinds of scientific analysis proceed by reducing the full richness of reality as we experience it to simpler quantitative concepts, and corresponding data in which patterns may be discerned and explained. So in what ways might ecology as a science really be more holistic – or less reductionistic – than, say, physics? This paper begins from an interpretation of both physics and ecology as comprising various kinds of models based on entities and quantities abstracted from the world of human experience – including a special class of model known as *scientific laws* that describe measurable relationships among variables and can be used to make predictions. In view of the complexity and interconnectedness of living systems, some might then imagine that ecology's subject matter prevents it from being as successful in this enterprise as the physical sciences, drawing attention to how few its laws are and how limited in scope and accuracy. Others, taking the view that laws of physics actually control the Universe, imagine that ecology's laws could only be curious instantiations of these real causal *laws of nature*: useful approximations to unpalatable equations, perhaps, that may be convenient for certain applications. We dispute all this. The view advanced below recognises a range of complementary types of abstraction across the sciences and appreciates a wide diversity of valid modes of scientific analysis and explanation, while denying that scientific laws constitute causal explanations. This leads to a new view of how to assess the holism of ecology and other sciences, regardless of their subject matter or ideological associations.

Law is a contested term with many connotations. The root meaning is probably a decree by which a governor regulates the way people go about their lives. When 'laws of nature' were conceived by early European natural philosophers such as Descartes and Boyle, the concept inherited much from the prominence of law in the Hebrew scriptures, where God is described as both making (e.g. Psalm 104, ESV) and respecting (e.g. Jeremiah 33:20, ESV) laws for the whole created order: inanimate, animate and human. With the advent of secularisation, the apparently inviolable nature of the laws for inanimate beings such as rocks and heavenly bodies (miracles aside) led some philosophers to the vision of discovering a set of true laws that would be equivalent to causes. However, that view largely gives way to a descriptive concept of scientific laws: the one often attributed to Isaac Newton. Newton's mathematical descriptions of relationships among abstract quantities such as mass, force and velocity helped establish an empirical tradition of 'laws of physics' that need not be taken as causal explanations. Such laws were hypothesised, inferred (not deduced) and provisional. This is the basic sense in which we will use *law* (some readers might prefer *regularity*), and in the next section below we begin sketching a framework for some different classes of law, with examples from physics. Since ecology is very different from physics, the section then gives some introduction to ecology and why its laws might look different.

The central section of this paper then builds our framework more explicitly by exploring candidate ecological laws under four modes of analysis, according to the types of quantities they relate. Then in the following section a formal view of abstraction is laid out, drawing upon the framework of the Dutch philosopher Herman Dooyeweerd. Distinguishing abstraction from reductionism suggests new perspectives on the types of laws that may most fruitfully be sought in ecology. This leads on, in the final section, to some suggestions for the development of a truly holistic ecology.

LAWS VIA ABSTRACTION IN PHYSICS AND ECOLOGY

We begin by laying out a view of the relationships between laws and several other categories of ‘model’ (Fig. 1). Scientific laws are often expressed as equations and so may be seen as a simple kind of mathematical model. They are often devised under the influence of conceptual models – such as the wave model of light, the organismic model of the plant community or the model of mutation and selection to explain evolution. We will return to conceptual models later, along with the notion of causal *laws of nature*. Mathematical models, meanwhile, may be classified into analytical and simulation models, each of which occupies a significant area of ecological research. Inferences may be deduced analytically or inferred from iterative simulations, by putting assumptions into mathematical forms and combining them. Dependence on multiple assumptions (Hall 1988), however, generally prevents such inferences from being taken as laws – rather as we distinguish Hubble’s Law (based on observations) from George Lemaître’s calculation of such a relationship (analytically modelled) on the basis of the theory of General Relativity and a model of cosmic inflation (Livio 2011). The challenge in demonstrating the scientific relevance of any kind of model lies in satisfying a scientific community that its assumptions are met in some situation of theoretical interest, and for a candidate law, this may generally be done by demonstrating that the relation holds for sets of empirical observations drawn from a sufficiently wide range of situations. The difficulty of achieving this in a world of complex interactions may explain why so much ecological work has been devoted instead to other kinds of modelling. In this paper, nevertheless, we focus on descriptive laws as one of the scientific elements that is easier to define and recognise.

[Figure 1 about here]

A perspective on the development of physics out of natural philosophy, with the accompanying accumulation of proposed laws, will provide both background and contrast for our proposal for ecology. Danie Strauss (2010) provides an illuminating account of physics by focusing on levels of abstraction. The abstraction of numbers and numerical relations in the foundation of classical mathematics is an enduring legacy of ancient philosophy and arguably the ground of much subsequent success in the empirical sciences. Where observation-based theorising was pursued, however, inadequacies of this *rational* mode of explanation gave place to a spatial mode involving irrational numbers and geometric relations – as employed in classical astronomy, for example. That the laws of geometry are not now considered part of physics perhaps underscores the foundational significance of the novel modes of explanation that followed. Indeed, in much of Descartes' natural philosophy the spatial mode remains predominant, and it is notable that the abstraction of space-filling corpuscles serves as a model of the Universe. But Descartes also draws upon a clear concept of motion, and especially with the work of Galileo and Newton, a kinetic mode of explanation emerges as dynamic relations become a fundamental phenomenon, and laws were formulated describing trajectories, velocities and accelerations. Then, under the paradigm of thermodynamics, laws were formulated to describe the irreversible flows of heat and its interconversion with work, and energy came to be abstracted as a very general property of fluids and other bodies. Next, with quantum mechanics, electromagnetic radiation and subatomic particles come to be abstracted along with properties such as wavelength and spin, subject to laws of particle physics. Meanwhile Einstein's work led to the abstraction of a mass–energy equivalence and the concept of spacetime, accompanying the laws of relativity.

In this view, physicists have always observed the behaviour of non-living bodies, but abstraction at different levels has multiplied both the classes of entities and the number of quantities described by its expanding list of laws. Today's physics student must learn to abstract such entities as bodies, subatomic particles and waves, and such quantities as momentum, charge, spin and spacetime. And whatever may be said about progress across paradigms, the laws of physics do mostly remain useful. For example, engineers may still make widespread use of Newton's laws of motion when dealing with discrete bodies, and of thermodynamic laws when dealing with fluids.

A scientific law, then, describes a quantitative relationship among certain abstract quantities that apply to a corresponding class(es) of ideal entity and that hold under given conditions (or with provisos). It should reliably provide both explanations and predictions. For ecology to adopt this definition, however, some details and potential objections need to be addressed. We will do this by considering each element of our definition in turn – and we hope, in the process, to absolve ourselves of the charge of 'physics envy' sometimes levelled at approaches like ours.

First, take the definition's core: quantitative relationships among abstract quantities. It must be noted that 'quantitative' may include statements of equality or directed inequality among variables – as in the second law of thermodynamics. There are also what may be called meta-variables, which determine the meaning of other variables. Scale is perhaps the most important of these in ecology: the prevalence of heterogeneity and fluctuation means that quantities must usually be measured as an average over some region or time-period, and the value of the latter can greatly influence the measurement obtained. Accordingly, the set of candidate variables that may be combined in ecological laws is unlikely to be a limiting factor; conversely, the search for unifying theories looks tougher.

Second, the classes of entity to which laws may pertain are if anything even more prolific in ecology, since biologists have expended considerable effort in classification projects. Species and organism are two particularly important general classes about which we will say more in the next section. Such classes may also be grouped in various hierarchies, from species up to kingdoms and from organisms up to ecosystems, items at various levels forming classes with their own properties. Moreover, ecologists may need to take into account the genetic diversity of individuals, seeing them as products of ontogenetic and phylogenetic histories. Mayr (1959) suggested that the uniqueness of ecology and evolution lies in their need for 'population thinking', i.e. considering differences among items – whether species or organisms – more than similarities. This variability is another reason why the choice of appropriate scales is important. It also calls attention to the fact that laws describe ideal entities. The entities described by laws of physics are such simple concepts as point charges, ideal gases and closed systems, which often appear good approximations to real things that physicists can observe; indeed electrons and other types of fundamental particles are observed so indirectly that they are simply assumed to be identical and ideal. But variation among individuals makes the subject-matter of biology difficult to idealise, and so less amenable to accurate description by laws. In summary, the multiplicity of ecological classes and the variability of entities within them calls for a very different approach from that of the physical sciences. Ecological laws may need to be less reductionistic in the sense of incorporating more information about individual differences.

The final element of the definition to tackle is that of conditions and provisos. The celebrated universality of laws of physics is in fact qualified: while they may well be applicable in all parts of the Universe for all time, this comes at the expense of *ceteris paribus* assumptions that generally require conditions to be unrealistically monotonous (e.g. 'if no other forces act'; 'at constant temperature')(Colyvan and Ginzburg 2003). But organisms evolve and function ecologically in intimate connection with particular environments, such that *ceteris paribus* clauses ('all else being equal') can simply never be true: inumerable aspects of the environment may influence what is observed and their states cannot be fixed. We cannot, therefore, require that laws of ecology make very accurate predictions. Indeed, we may not even wish to imagine a biological experiment so well controlled that laws of biology would be accurate with good precision, for it might amount to killing the object of study, making biological laws irrelevant altogether. Cooper (2003, 113) suggested that an ecological law merely has to hold across a range of conditions large enough to be useful. Also, in view of ecology's focus on natural kinds (e.g. alleles, species and communities), we may allow some of its laws to apply only to certain classes of entity. On the other hand, since natural kinds can be extremely diverse and are not held to be immutable, useful laws should apply to broad classes, such as the whole plant or animal kingdom on Earth, if not to all living things conceivable.

Where provisos become prohibitively restrictive, an analytical shift is called for. One option is to look at different scales (Henle et al. 2014). Ecologists have always been constrained by logistical and computational limitations – but perhaps also beguiled by reductionist perspectives encouraging a focus on small areas and short time-horizons. Thus it took almost a century before individual behaviour was properly considered in studies of animal demographics, with a corresponding increase in study scales (Levin et al. 1997). Similarly, early work on ecological communities focused on fine scales now enlarged in the light of understanding gained from studying landscape and even continental scales, along with global samples of species (Lessard et al. 2012). Making observations or analyses at a broader scale can, by the law of averages, reduce the unexplained variability (random noise) in quantitative relationships that are simultaneously influenced by many other factors. Ecological research is painstakingly slow, and decades may have been lost under research focused on scales too small for proper recognition of the forces at play. Accounting for larger time-scales takes even longer, and the value of long-term experiments has been appreciated more slowly, for obvious reasons. Nature works at great scales, and so must we.

Increasing scales alone, however, does not necessarily bring success (Botkin 1977). The search for more general, resilient laws may be further aided by the use of different kinds of abstraction. Newtonian mechanics is not generally used to study the dynamics of fluids, nor electrostatic theory to explain chemical reactions. Such mismatches can occur in ecology, as we show in the next section.

CONTEMPORARY ECOLOGICAL PARADIGMS AND THEIR LAWS

Both practitioners (Lawton 1999; Murray 1992; Poulin 2007; Southwood 1980) and philosophers (Cooper 2003; Ulanowicz 2009) see a gulf between the reality of ecological science and the picture presented by 20th-century philosophers of science (often just philosophy of physics). They express varying degrees of unease at the fact that regularities in ecology seem hard to come by, and any laws acknowledged appear to be contingent, limited in explanatory power and unable to predict accurately. Sharing the unease, we believe the poverty of laws is partly for the reasons outlined in the previous section. We also agree with Lawton (1991) that there is insufficient interaction among ecology's major methodologies: arguably theoretical ecology has explored mathematical relations with limited opportunities to test their applicability to ecological systems, experimentation has been severely restricted in the spatial and temporal scales at which underlying processes are probed, and statistical ecology has been dominated by null-hypothesis tests designed to ask merely whether observed patterns are consistent with randomness or not. Some ecologists have launched profound critiques of the ways in which ecology is pursued as a science: both Peters (1991) and Murray (1992) complain of the failure to produce predictive laws. Perhaps our science is deemed holistic simply because it is messy!

We believe there is more to ecology than has so far met the philosopher's eye. Just as a suite of alternative modes of analysis and explanation has unfolded historically in the physical sciences and remains useful for various applications, so it appears that a similar suite is displayed contemporaneously in the diverse practices and theories comprising the science of ecology. This may be illustrated by describing a set of four distinct ecological modes of analysis that yield different types of laws and suggesting some of the outstanding candidates for laws of ecology that are proposed within each. We use the term *paradigm* here loosely and in the broad sense of a set of a set of examples, concepts and methodologies used by a community of researchers. We will say more about the corresponding modes of explanation later.

The population paradigm

Since early last century the population paradigm has built upon basic organismal biology – concerning species' physiology and life-histories – with the study of population dynamics (Nicholson 1933). This paradigm primarily focuses on the abundances of single biological species, or pairwise interactions between species. The individual is a fundamental concept in biology, but it is nevertheless an abstract class of entity (Fig. 2). Recognising individuals in practice is relatively straightforward in the case of most animals but often less so for plants, which may be clonal and spread vegetatively; a hint of reductionism may already be seen in abstracting individual grass plants from a meadow, for example. Then, given a method of enumerating individuals, population sizes can be abstracted by applying the biological species concept (Mayr 1942). This too may be fraught with conceptual challenges, but armed with a working definition and search-image of a species of interest, an experienced ecologist can assess the numbers of individuals within a specified region (classically populations are considered as closed to migration). Dividing such counts by the area or volume of the region then yields population densities, which are the focal quantity in population-ecology studies. Such densities may be compared over time or space and mathematically related to each other.

The main universal law proposed in this paradigm is that of density-dependence. This states that in any given system (specified location and species), there is a density known as the carrying capacity above which populations tend to decline and below which they tend to increase. The determinants of this density, the rate at which it is approached and the nature of fluctuations around it are modelled in terms of density-dependent dynamics (Hixon, Pacala, and Sandin 2002), with empirical data being used to estimate free parameters for each of these details. When there are one or more parameters that must be estimated from data in any given situation, we may speak of a ‘weak law’, since it can only be used for making predictions once the parameter(s) are believed to be correct. A class of laws in this paradigm pertains to the prediction of carrying capacities in particular kinds of system (Peters 1991, 275). Arguments have raged from the 1940s (Nicholson 1954) and 1960s (den Boer 1968) through to the 21st century (Berryman 2002) about the true nature and role of density-dependence in population ecology, but one of its defining assumptions is the ideal of the closed population.

Other laws emerge from the idea of the metapopulation. Metapopulation models simulate how discrete patches of habitat alternate between being occupied and unoccupied by a species according to demographic stochasticity and migration rates between the patches (Harrison and Taylor 1997). It has been shown that long-term stability may pertain without assuming any form of density dependence: the mathematical definition of metapopulation capacity implies a law of persistence based on basic demographic properties (Hanski and Ovaskainen 2000). Such models are not explicitly spatial, although they are only realistic when assumed to describe population patches spread over much larger areas than those modelled using classical density-dependence. Indeed, ecology is replete with laws and phenomena that apply at particular ranges of scale (Levin 1992).

The population paradigm can extend to a multi-species analogy. Scaling up from populations of individuals to populations of species, neutral community models consider speciation and extinction in place of birth and death. ‘Neutral’ here means that species are considered as equivalent to each other: individuals are ‘species-blind’, interacting with each other and their environment in the same way regardless of what species they belong to. An observer can distinguish them, and they reproduce after their own kind, but in simple neutral models there are no specific habitat preferences or competitive interactions. The unified neutral theory of biodiversity and biogeography

(Hubbell 2001) explores the statistical implications of assuming functional equivalence of all species in a community, giving predictions of relative abundance distributions for large numbers of anonymous species and their expected lifetimes.

The population paradigm, in summary, considers abundances in fixed spatial regions, so that it can be seen as primarily numerical. A classic statement of this paradigm is John Harper's address to the British Ecological Society (1967): "A Darwinian Approach to Plant Ecology".

[Figure 2 about here]

The macroecology paradigm

What we call the macroecology paradigm is fundamentally geometrical. With roots going back nearly two centuries (Watson 1847), analyses of spatial patterns have gathered momentum in recent decades with advances in probability theory and computational possibilities (Smith et al. 2008). This paradigm typically focuses on the patterns of multiple species across large extents of space and sometimes time (Fig. 2). Important laws of the spatial-ecological paradigm relate numbers of individuals, of species and of endemic species to variable areas of observation – which may be isolated, contiguous or nested (Scheiner 2003). The theory of island biogeography (MacArthur and Wilson 1967), seminal in this paradigm, was largely heuristic: when the area of islands and the corresponding numbers of species found on them are both log-transformed, data points tended to cluster around a straight line. It has since been shown how species–area relationships for islands of varying area can be derived mathematically by combining the principles of random, distance-dependent migration of individuals with demographic stochasticity (Hanski and Gyllenberg 1997), and how a range of relationships among numbers of species and areas in contiguous space arise from principles of local dispersal of distinct species (Chave and Leigh 2002).

The macroecology paradigm has been highly successful in generating laws relating its own fundamental quantities to each other. While the laws are typically weak, having at least one free parameter to be tuned to fit empirical data, typical ranges of some parameters have been characterised, increasing the scope for making predictions. For example, species–area relationships typically follow a power-law with exponent between 0.15 and 0.4, for plants as well as animals – the lower end of this range being typical for islands, smaller organisms and higher latitudes (Drakare, Lennon, and Hillebrand 2006). A contemporary statement of the paradigm's success may be seen in the celebration of unified theories of biodiversity (McGill 2010). Here Brian McGill focuses on mathematically unifying six theories that each ‘unify ideas of area, abundance and [species] richness’. But because the latter is commonly presented as ‘biodiversity’, the paper might be naively taken to present *the* unified theory of ecology!

Despite its name and fanfare, we might after all question how far the macroecology paradigm is intrinsically ecological. Its focus on spatial and numerical abstraction (Caswell 1976) is such that its laws are not necessarily specific to living organisms: they might equally well describe spatial patterns of types of non-living artefacts, or in human cultural systems (e.g. Bentley, Hahn, and Shennan 2004) – and indeed a proportion of its significant papers are published in physics journals (e.g. Blythe and McKane 2007). While proponents of the paradigm may see this as a mark of success, this must be tempered by the limited kinds of quantities that can be predicted – which are mostly numerical and spatial. A similar charge may be laid to the population paradigm: its predictive quantities are essentially counts of things (individuals, species or occupied patches), and some of its laws might conceivably apply to non-biotic entities such as molecules in chemical reactions (e.g. Sadownik et al. 2016).

Thus the contrast between the population and macroecology paradigms should not be overplayed. They have in common a focus on the individual and its species identification, and many studies span both paradigms, as exemplified by the literature on spatial density-dependence (e.g. Gunton and Pöyry 2016) and spatial neutral models (Rosindell and Cornell 2007). We now turn to a pair of paradigms in which the species concept serves as no more than a tool.

The ecosystemic paradigm

The ecosystemic paradigm originates with the project by Tansley (1935) to use concepts from physics to understand ecological processes. As such, it defines the *ecosystem* to include non-living features along with the biotic. This *abiotic environment* is, of course, biotically referenced; it concerns those physical features that are known (or hypothesised) to affect living organisms, such as temperature, light and chemicals with which living tissues may interact. This paradigm can also absorb the ambiguity over whether morbose or detached tissues are living or not (Lindeman 1942). Integrating living and non-living elements for scientific analysis entails a focus on the highest common mode of functioning shared by these elements, which is physical. Thus quantities routinely abstracted in the ecosystemic paradigm include biomass, carbon pools, chemical concentrations, energy flux rates, evaporation rates and temperature. Such quantities are attributed to ecosystems and specified compartments within them, although in practice this is often done by drawing upon data attributed to individual organisms and species. The aim is to abstract to a level beyond the complexities of interactions between specific individuals in order to assess emergent behaviours and attributes. These typically include such complex concepts as net primary productivity, evapotranspiration, rates of nutrient cycling and food-web complexity.

Candidate laws connecting ecosystem variables are not difficult to find insofar as empirical relationships are regularly quantified in ecosystem studies. Their predictive power is rarely impressive, however (Reichstein et al. 2014). The ecosystemic paradigm presents challenges for ecologists in search of laws more than any other paradigm: its variables are difficult to measure and highly sensitive to scale, its entities are difficult to observe and define, and the conditions that might need to be specified as provisos can rarely be controlled or found in steady states. Weak laws have, nevertheless, been formulated relating ecosystems' productivity, disturbance and diversity, as well as relationships of these variables to soil nutrient concentrations and rainfall. Examples include resource response models such as the equations relating overall chlorophyll concentration, plankton biomass or primary productivity to the total phosphorus concentration of a lake (Table 10.1 in Peters 1991), the intermediate disturbance hypothesis, which states that the species richness of a site will be maximised at intermeidate intensities of disturbance (Wilkinson 1999), and the productivity–fire relationship, stating that fire intensities are greatest at intermediate levels of habitat productivity (Reich et al. 2001). Such laws have mostly been arrived at heuristically, through empirical observation of variables of interest at a range of spatial and temporal scales, followed by statistical parameterisation.

This paradigm offers great scope for selecting appropriate scales and levels of abstraction, and perhaps the best statement of its potential is made by Robert Ulanowicz (2009).

The trait paradigm

The paradigm of trait-based ecology has risen to prominence in the last few decades but sits in historic continuity with the wider science of biology. This paradigm concerns the abstraction of functional traits (Fig. 2): properties that may be measured across a wide taxonomic range of individuals, that may be standardised to some degree and that are hypothesised to relate to the survival and reproduction of the organism (McGill et al. 2006). They typically include standardised measurements of specified organs and their chemical composition. While such quantities may also feature in other paradigms, the trait-ecology paradigm is distinguished by its search for general principles or rules applying across many species (McGill et al. 2006). For example, comparisons of species' trait attributes (specific values of traits) were central to the development of niche theory.

The competitive exclusion principle (Gause 1934) suggested that only one species could occupy a given niche, leading to the hypothesis of some degree of limiting similarity in the attributes of pairs of species that could coexist (den Boer 1986). There were attempts to quantify this limiting similarity (Rappoldt and Hogeweg 1980), but attempts to find a general law largely failed (Wilson, Gitay, and Agnew 1987).

More successfully, various schemes have been proposed for relating the relative values of suites of functional traits to each other across different species and habitats. The idea of arranging species along a spectrum according to their tolerance of disturbance (MacArthur and Wilson 1967) was combined with the concept of adversity selection (Whittaker 1975) by Southwood (1977), who proposed a habitat-based 'template' for ecological communities defined by two fundamental axes: the predictability and the favourability of habitats (Greenslade 1983). The C-S-R theory of primary strategy types for plants (Grime 1974), and more ambitiously for living organisms in general (Grime and Pierce 2012), takes a similar approach but proposes three fundamental axes. Habitats conducive to vigorous competition are expected to exclude stress-adapted and short-lived species, while stressful and disturbed habitats support only stress-tolerant and ruderal species respectively. Here we notice the use of trait attributes to abstract functional types: analogues of biological species. An important step towards operationalising the C-S-R theory was provided by the discovery of the leaf economics spectrum (Wright et al. 2004), which appears to describe Grime's competitor–stress-tolerator axis for plants in terms of correlations among six leaf traits. Since the analysis by Wright et al. (2004) was based on a global dataset of higher plants from a wide range of habitat types, quantitative relationships it described may meet the requirement for universality of laws. Let us consider the relationship with the greatest degree of correlation as a test case. This relates logarithms (in base 10) of nitrogen to phosphorus concentrations in leaves (respectively N and P, both in %) as: $\log N = 0.83 + 0.66 \log P$ – i.e. a 4.6-fold change in nitrogen concerntration per 10-fold increase in phosphorus, with covariance of 0.72. This indicates a non-linear relationship: the ratio of nitrogen to phosphorus concentrations increases with increasing nitrogen concentration. Earlier work had suggested that the ratio was typically around 10 (Garten 1976) and recognised effects of nutrient limitation, but that law can now be replaced by this more comprehensive one. Analogous laws have been proposed for various wood traits of woody plants (Chave et al. 2009), and there has been discussion of a more general 'plant economics spectrum' (Freschet et al. 2010).

It is true that this statistical–empirical approach could be pursued to the point where a 'law' is discovered every time a statistical model is fitted to data from a broad enough data set (Peters 1991), and some rates of decline in accuracy with increasing scope may be too precipitous to be acceptable. The following is an example of a more theory-driven case – which also brings the possibility of pre-specifying the kinds of conditions in which a law should most clearly be observed. The fact that metabolic rates tend to scale as a function of body-size raised to the power of about three-quarters ($B^{0.75}$), for of all kinds of organisms, had been known for a long time without a satisfying explanation (Feldman and McMahon 1983) until West, Brown, and Enquist (1997) published a metabolic scaling theory that explains this relationship in terms of the physics of fluid flow. Indeed, their theory also predicts observed body-size dependencies for rates of cellular metabolism, heartbeat and maximal population growth (all $B^{-1/4}$), and time periods of blood circulation, embryonic growth and life-span (all $B^{1/4}$) (West, Brown, and Enquist 1997). Various other physiological laws might also be cited here (Peters 1991, 281).

As mentioned earlier, openness of paradigm boundaries means that some successful work straddles more than one paradigm. Laws for body-size–abundance distributions in animals (referenced in Peters and Raelson 1984), for example, combine a trait with a spatial quantity to achieve moderate predictive power with broad applicability. The trait paradigm, however, is particularly characteristic of ecology, and we suggest that its development will be crucial to the future of the science – not to mention its public appeal. There are many contemporary statements of its scope (Verberk, van Noordwijk, and Hildrew 2013; Winemiller et al. 2015).

MODES OF ANALYSIS AND ASPECTS OF REALITY

Our brief survey of four ecological paradigms (summarised in Table 1) reveals some fundamentally different concepts among them. It also suggests that while laws have been proposed mostly in the population and macroecology paradigms, which are mathematically-oriented, there is great scope for general laws to be specified in the more ecologically oriented trait and ecosystemic paradigms. A quantitative study along these lines has in fact recently appeared: Linquist et al. (2016) analysed the prevalence of ‘resilient generalisations’ in ecology by comparing published meta-analyses concerning the three areas of population, community and ecosystem studies. Statistically-significant effects were registered in around 80% of the 187 meta-analyses used, and the finding that average sample sizes, numbers of taxa and numbers of biomes were broadly similar was taken to indicate comparable levels of generality for candidate laws in the three areas of ecology. Comparing actual degrees of scope and predictive accuracy among our different paradigms would be an illuminating exercise.

[Table 1 about here]

It may be asked why the four paradigms we have identified should be so significant. An answer may be given after synthesising a number of proposals made so far. We have suggested that scientific analyses depend upon abstracting classes of entities and quantitative properties from real-world situations observed by scientists. We have affirmed the *descriptive* definition of scientific laws as resilient relationships among such quantities when predicated of ideal entities – whether they describe the numbers of fundamental particles in atoms or the density of individuals in types of habitat, the locations of planets or living organisms in 2- or 3- dimensional space, or the energy of fluids in containers or energy flow rates in ecosystems. Finally, we have suggested some distinct modes of analysis as a basis for distinguishing scientific paradigms. Our synthesis of these proposals draws upon the framework of the Dutch philosopher Herman Dooyeweerd, who suggested building a systematic understanding of reality upon the recognition of multiple fundamental nuclei for the human faculty of abstraction (Dooyeweerd 1953). Dooyeweerd's list of modes began with the categories numerical, geometric, kinetic, physical, biotic and sensitive. For example, gathering data on tree seedlings in a forest, one might abstract the concepts of number in counting individuals, of height and location in measuring them, and of disease and death in examining their tissues. Asked what kind of variables were collected, we might summarise these respectively as numerical, spatial and biotic variables concerning the seedlings. This summary abstracts three broader categories, of the kind that Dooyeweerd termed 'aspects' of reality.

According to Dooyeweerd, one cannot meaningfully abstract further to unify, say, the numerical and spatial aspects, the spatial and biotic, or all three. The intrinsically biotic properties of a situation cannot be explained by the spatial, for example, or *vice-versa*. Attempting to substitute any of these aspects for any other without loss of meaning is reductionistic in a way that Dooyeweerd showed to be experientially incoherent; such attempts deprive the concepts of their intuitive meanings (Dooyeweerd 1953). The existence of distinct kinds of laws for spatial, physical and biotic properties may also be suggested by the distinct natures of biology, physics and geometry; while each discipline in this list depends upon concepts drawn from the following ones, the converse is not true; moreover, these sciences tend to remain separate in the structures of academic institutions. The distinction of the aspects has been argued elsewhere (Strauss 2009); for present purposes we simply draw upon them heuristically. While debate over the legitimacy of various kinds of reductionism will continue, we may fruitfully continue exploring the diversity of modes of analysis across the science of ecology under the suspicion that they reflect distinct aspects of reality.

The mutual irreducibility of a set of modes of analysis suggests an explanation for the coexistence of such contrasting paradigms as we find in contemporary ecology. While the population-ecology paradigm assumes certain intrinsically-biotic concepts such as reproduction, maturity, death and competition, these are simply reduced to multiplicative coefficients in most work so that the main focus can be numerical. Accordingly, its laws and other outputs generally concern *population* sizes, structures and extinctions – outputs useful enough for purposes of population management, such as species conservation. Similarly, the macroecological paradigm is focused on spatial as well as numerical properties. Accordingly, geometrical *patterns* are what its laws can predict – and useful for biodiversity management. Indeed, this paradigm also seems to cover the temporal biodiversity patterns studied in paleoecology. The ecosystemic paradigm again involves biotic abstraction, but its focus is those physical quantities that can also capture dead and non-living components of a *system*. Its special concern with processes may also reveal a kinetic mode of analysis concerning fluxes, states and changes, which concepts Dooyeweerd attributed to a distinct ‘kinematic’ aspect of reality. The outputs of the ecosystemic paradigm can be useful for management of land and water bodies as well as the increasing challenge to manage global climate. The trait paradigm, finally, is directly focused on biotic phenomena. It seeks laws to describe biotic functions occurring within and between organisms, and its outputs should be useful for such diverse interests as the improvement of agricultural cultivars, understanding of invasive species’ behaviour and biological impacts of extinctions. Like the other paradigms, it has its blind-spots and may be combined with different paradigms for certain purposes. In summary, each paradigm answers certain kinds of questions and has different contributions to make in the application of ecological science to the challenges identified by society.

The postulate of distinct kinds of abstraction may also suggest an evaluation of the history of particular sciences and hypotheses for future work.The account of physics with which we started portrays progression along Dooyeweerd’s sequence of modes of abstraction, and leaves open the possibility that there might even be further aspects of reality to disclose in the study of non-living things (the framework was expected to be developed and refined: Dooyeweerd 1953, vii) – a question that we must leave to philosophers more active within that field. The ecological story is not so evidently progressive; indeed its notable abandoned paradigm – the organismic model of communities – is decidedly biotic in emphasis (Clements 1916, cited in Keller and Golley 2000), and it seems unlikely that the population, macroecology and ecosystemic paradigms will come to be seen as precursors to the functional trait paradigm. Instead, one might see the coexistence of paradigms as a healthy part of such a holistic science. After all, it is clear that earlier paradigms of the physical sciences are by no means dead, and that many scientific laws have enduring validity.

Ecology might be so much the richer for its privileged position, able to draw upon a range of modes of abstraction. Here, following Dooyeweerd's sequence on to the sensitive aspect, we should also mention the science of behavioural ecology as a paradigm partly focused on the sensitive perceptions of animals.

To draw together the challenges of prediction and explanation, the meaning of 'reductionism' should be clarified. 'Reduction' is sometimes used to mean what should be called abstraction. Abstraction is surely an essential – even foundational – component of the sciences, whereas reductionism tends to imply a simplistic notion of causation (Levins and Lewontin 1980). 'Reductionism' thus remains problematic for the reasons given above, as reflected in the term 'greedy reductionism' [Watts & Reiss, this issue], and we suggest that recognising a legitimate plurality of modes of analysis in ecology should guard against this. But we can also take modes of analysis to provide modes of explanation, as suggested by Strauss (2009, 402-416). A brief look at ecological modes of explanation will help conclude our survey. That is, how do scientific laws relate to conceptual models?

Likening a complex situation to something more familiar is the basis of many a scientific explanation, as suggested by the predominance of metaphors in scientific terminology. Ecology is replete with these: populations and their carrying capacities; communities, assemblages and systems; competition, stress and disturbance; and traits and their filters are just some prominent examples. The analogies behind these metaphors sometimes suggest causal analogues that may be influential in theorising about a topic. *Carrying capacities* suggest volumes of containers that can hold certain numbers of items and spill if over-filled – and so the law of density-dependence may gain a mechanical connotation that seems, to most ecologists (let alone laypersons), to provide a more compelling causal analogue than any notion of causation acquired from watching the births, struggles and deaths of moths or fruit flies in jars of medium. *Trait filters* suggest a sieving process (sometimes directly illustrated – e.g. Keddy 1992) in which certain trait values are admitted to a collection while others are excluded – and so laws of community composition similarly gain a mechanical connotation that provides a compelling causal analogue. Indeed, most of the above metaphors concern mechanical analogies, which prompts the question whether ecologists' conceptual models are predominantly physical (competition may be the exception in the above list) – and if so, why. A detailed study of the diversity of conceptual models in ecology and their relationships to ecological laws would no doubt be illuminating. For now, we may surmise that the predominance of mechanical metaphors and imagery in conceptual models makes up for the relatively small contribution of the physical (ecosystemic) paradigm to ecology's laws. Thus, as modes of explanation, the paradigms must complement to each other if one is not to displace the others.

A TRULY HOLISTIC ECOLOGY

Contemporary ecological science employs a range of levels of abstraction – manifested in both its analytical laws and its conceptual models – and analyses phenomena at a range of scales. Our vision for ecology as a holistic science, then, may be grounded in three features. First, ecology gradually refines its focus to appropriately-broad spatial and temporal scales of analysis within each of its paradigms. This is perhaps comparable with the inclusion into physics of such concepts as action at a distance and statistical mechanics. Second, a portion of its theory (and laws) is based on abstractions that can only be made of living things. This means not only abstraction of biological classes (common to all the paradigms), but also of essentially biological quantities such as demographic rates, speciation rates and trait values. More generally, we might say that ecology sometimes employs the least reductionistic mode of analysis consistent with its subject matter – and in this sense contemporary physics, with its understanding of energy, is also more holistic than Newtonian physics. Thirdly, it is significant that ecology accommodates a range of complementary modes of analysis, focusing on what may be conceived of as the numerical, spatial and physical aspects of reality as well as the biotic. It has been claimed that community ecology could be logically and mathematically reduced to population ecology, and that in turn to 'individual ecology' (Schoener 1986), and this may be plausible within areas of those three programmes concerned with abstraction at the 'mechanistic' (*physical*?) level; indeed the claim appears trivial if considered merely at the spatial level (since the macroecology paradigm can well work with neutral species). But a claim that the trait, ecosystemic, spatial and population paradigms might be mutually reducible cannot even be entertained, we suggest, without denying the fundamental concepts of organisms, flows, patterns and counts as we intuit them. These concepts are not differentiated simply by scaling, as sometimes claimed; they are logically incommensurable (Clouser 2005, 192f). This view of ecology's holism may now suggest some ways in which the versatility and usefulness of the science may be enhanced by balancing different research paradigms under such a vision.

Our view may be summarised by three distinctive proposals. Firstly, ecology can and should have its own laws, and these may be discovered quite heuristically. Quantitative relationships among variables abstracted at appropriate levels and measured at appropriate scales are legitimate candidates for laws of ecology, and the community will determine which ones are sufficiently robust to be accepted as such. Secondly, our four modes of ecology offer a robust alternative to the typical major divisions of ecology textbooks. Textbooks commonly distinguish population, community and ecosystem ecology, treating macroecology (if at all) with evolution and trait ecology rather haphazardly; one of the most popular textbooks reveals a particularly individual-focused emphasis in its tripartite division into “Organisms”, “Species interactions” and “Communities and Ecosystems” (Begon, Townsend, and Harper 2006). Thirdly, our view supports broader philosophical challenges against both reductive physicalism and holistic vitalism. The notion of physical mechanisms being the ultimate model of causation leaves ecology as a peripheral and inescapably complicated science (Colyvan and Ginzburg 2003) where *chance* often has to be invoked as a pseudo-cause (Ulanowicz 2009). Vitalism (or idealist holism: Levins and Lewontin 1980), by contrast, tends to advance non-deterministic explanations – as in the organismic view of plant communities (Clements 1916, cited in Keller and Golley 2000). Our view, while agnostic about the locus of causation, expects a wide range of ecological phenomena to be broadly predictable under suitable analyses.

We end, then, with a plea for pluralism. Ecologists should celebrate the diversity of paradigms that make up our science and recognise that progress in theoretical and applied ecology will be enhanced by the use of modes of analysis appropriate for the applications envisaged. In particular we suggest that there will be room for strong laws and unifying theories in each of the main paradigms of ecology. Educators, meanwhile, might emphasise to students the distinctly biotic paradigm of trait ecology, perhaps even as their primary introduction to the science before numerical, spatial and physical paradigms. Finally, we hope that philosophers of science will recognise the diverse set of modes through which a holistic notion of causation may be refracted to yield complementary causal accounts, none of which is ontologically privileged – although some will invariably be more useful than others in any given situation. Further work on concepts of causation in ecology is called for (Bateson and Laland 2013).

If the proposal made here proves useful in the science of ecology, investigation along similar lines in the human sciences might uncover yet richer arrays of paradigms in holistic complementarity. In psychology, the longstanding opposition between unimodal and bimodal interpretations of the human mind might be overtaken by views recognising the complementarity of three or more modes for conceptualising and analysing the phenomena of human experience [REF?]. In the social sciences Dooyeweerd recognised the value of historic and linguistic aspects alongside a truly social one (Dooyeweerd 1953), and this scheme further recognises distinct economic, aesthetic and juridical aspects as being invoked in appropriate fields of scholarship.

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Table 1: Focal concepts and topics of the four ecological paradigms outlined in this article. Note that this set of paradigms is not intended to be exhaustive but simply to illustrate some alternative approaches to scientific abstraction in ecology.

	Population	**Macroecology**	**Ecosystemic**	**Trait**
Approximate synonyms:	Autecology; Species ecology	Neutral /near-neutral ecology	Process ecology	Comparative ecology; Synecology
Focal abstractions:	Population + Species	Spatial pattern + Species	Process + Community	Functional trait + Individual
Other fundamental concepts:	Life-cycle	Habitat patch	Resource fluxes	Niche; Functional type
Typical laws:	Density-dependence	Species–area relationships	Productivity relationships	Trait relationships
Fundamental questions:	Are population densities regulated?	What is the unified theory of biodiversity?	How do ecosystems interact with their environment?	How do different species coexist? Are there real types of communities?
Typical application:	Will this species survive in this region?	How many species will be found in this region?	How stable is this ecosystem?	Which species will be found in this community?
Aspect of analysis:	Numerical	Spatial	Physical	Biotic

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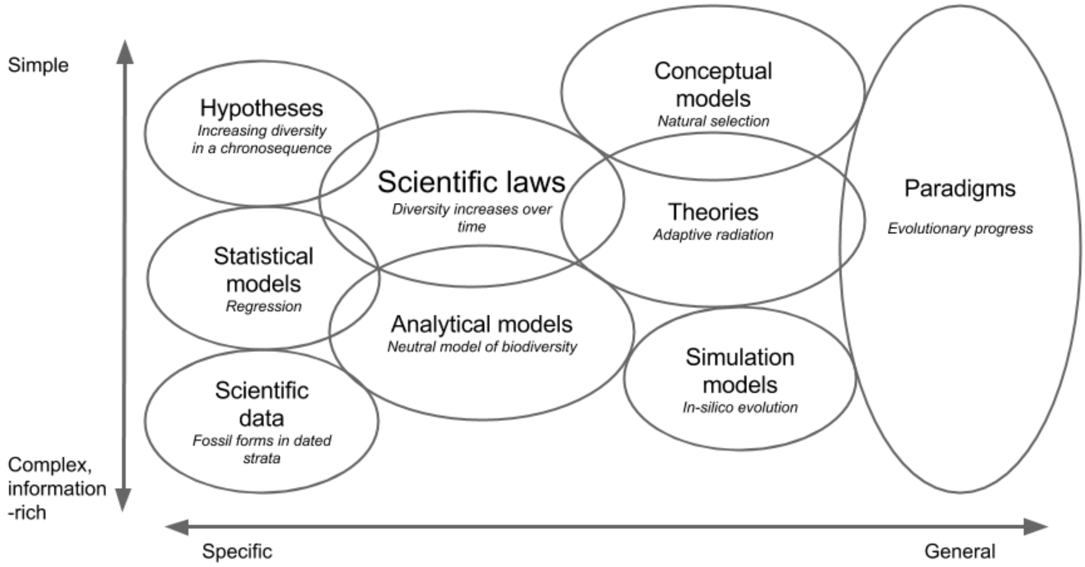

Figure 1. A conceptual map to situate scientific laws among a range of other concepts discussed in the text. These are ordered from the more specific (left) to the more general (right), and from the more complex (bottom) to the simpler (top). The contact and overlap among the ellipses are intended to suggest, respectively, degrees of conceptual proximity and semantic overlap. The italicised words in each ellipse comprise a set of examples taken from evolutionary ecology.

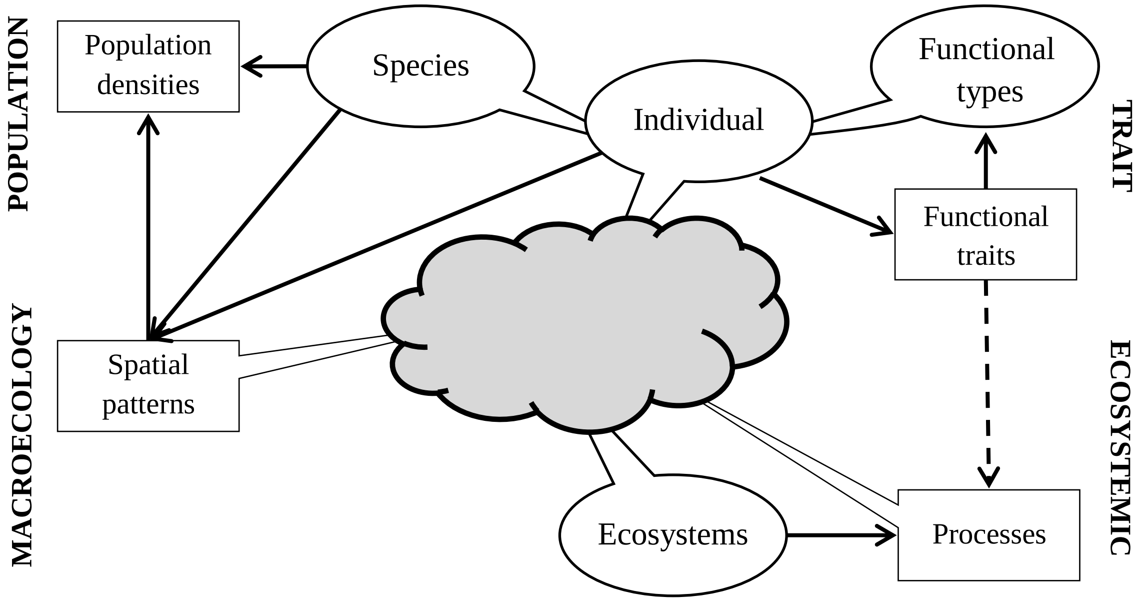

Figure 2. Schematic representation of modes of analysis employed in various ecological paradigms. The grey cloud represents the world of experience. The ellipses represent classes of entities abstracted from experience, while the boxes represent kinds of quantities abstracted, to which laws may apply. Arrows point from quantities or entities to others that they help to define. The four paradigms corresponding to the four focal quantities are given in upper-case letters adjacent to the relevant boxes.

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