

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

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10 **ABSTRACT**

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

23

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

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26

27 Ecology, as the study of general patterns in the relationship of organisms to their environments,  
28 appears to be a holistic science. This notion is no doubt bolstered by its links to an ideology. What  
29 English-speakers call *green* is rendered in many other languages as *ecological*, which (also in English)  
30 evokes the ethic of conservation and certain kinds of nature-focused worldviews and lifestyles that

31 reject reductionistic explanations and technologies. But all kinds of scientific analysis proceed by  
32 reducing the full richness of reality as we experience it to simpler quantitative concepts, and  
33 corresponding data in which patterns may be discerned and explained. So in what ways might  
34 ecology as a science really be more holistic – or less reductionistic – than, say, physics? This paper  
35 begins from an interpretation of both physics and ecology as comprising various kinds of models  
36 based on entities and quantities abstracted from the world of human experience – including a  
37 special class of model known as *scientific laws* that describe measurable relationships among  
38 variables and can be used to make predictions. In view of the complexity and interconnectedness of  
39 living systems, some might then imagine that ecology’s subject matter prevents it from being as  
40 successful in this enterprise as the physical sciences, drawing attention to how few its laws are and  
41 how limited in scope and accuracy. Others, taking the view that laws of physics actually control the  
42 Universe, imagine that ecology’s laws could only be curious instantiations of these real causal *laws*  
43 *of nature*: useful approximations to unpalatable equations, perhaps, that may be convenient for  
44 certain applications. We dispute all this. The view advanced below recognises a range of  
45 complementary types of abstraction across the sciences and appreciates a wide diversity of valid  
46 modes of scientific analysis and explanation, while denying that scientific laws constitute causal  
47 explanations. This leads to a new view of how to assess the holism of ecology and other sciences,  
48 regardless of their subject matter or ideological associations.

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

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

72

### 73 **LAWS VIA ABSTRACTION IN PHYSICS AND ECOLOGY**

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

93

94 [Figure 1 about here]

95

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

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

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

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

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

158 The final element of the definition to tackle is that of conditions and provisos. The celebrated  
159 universality of laws of physics is in fact qualified: while they may well be applicable in all parts of the  
160 Universe for all time, this comes at the expense of *ceteris paribus* assumptions that generally require  
161 conditions to be unrealistically monotonous (e.g. 'if no other forces act'; 'at constant  
162 temperature')(Colyvan and Ginzburg 2003). But organisms evolve and function ecologically in  
163 intimate connection with particular environments, such that *ceteris paribus* clauses ('all else being

164 equal') can simply never be true: innumerable aspects of the environment may influence what is  
165 observed and their states cannot be fixed. We cannot, therefore, require that laws of ecology make  
166 very accurate predictions. Indeed, we may not even wish to imagine a biological experiment so well  
167 controlled that laws of biology would be accurate with good precision, for it might amount to killing  
168 the object of study, making biological laws irrelevant altogether. Cooper (2003, 113) suggested that  
169 an ecological law merely has to hold across a range of conditions large enough to be useful. Also, in  
170 view of ecology's focus on natural kinds (e.g. alleles, species and communities), we may allow some  
171 of its laws to apply only to certain classes of entity. On the other hand, since natural kinds can be  
172 extremely diverse and are not held to be immutable, useful laws should apply to broad classes, such  
173 as the whole plant or animal kingdom on Earth, if not to all living things conceivable.

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

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

192

### 193 **CONTEMPORARY ECOLOGICAL PARADIGMS AND THEIR LAWS**

194 Both practitioners (Lawton 1999; Murray 1992; Poulin 2007; Southwood 1980) and philosophers  
195 (Cooper 2003; Ulanowicz 2009) see a gulf between the reality of ecological science and the picture  
196 presented by 20<sup>th</sup>-century philosophers of science (often just philosophy of physics). They express

197 varying degrees of unease at the fact that regularities in ecology seem hard to come by, and any  
198 laws acknowledged appear to be contingent, limited in explanatory power and unable to predict  
199 accurately. Sharing the unease, we believe the poverty of laws is partly for the reasons outlined in  
200 the previous section. We also agree with Lawton (1991) that there is insufficient interaction among  
201 ecology's major methodologies: arguably theoretical ecology has explored mathematical relations  
202 with limited opportunities to test their applicability to ecological systems, experimentation has been  
203 severely restricted in the spatial and temporal scales at which underlying processes are probed, and  
204 statistical ecology has been dominated by null-hypothesis tests designed to ask merely whether  
205 observed patterns are consistent with randomness or not. Some ecologists have launched profound  
206 critiques of the ways in which ecology is pursued as a science: both Peters (1991) and Murray (1992)  
207 complain of the failure to produce predictive laws. Perhaps our science is deemed holistic simply  
208 because it is messy!

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

218

### 219 *The population paradigm*

220 Since early last century the population paradigm has built upon basic organismal biology –  
221 concerning species' physiology and life-histories – with the study of population dynamics (Nicholson  
222 1933). This paradigm primarily focuses on the abundances of single biological species, or pairwise  
223 interactions between species. The individual is a fundamental concept in biology, but it is  
224 nevertheless an abstract class of entity (Fig. 2). Recognising individuals in practice is relatively  
225 straightforward in the case of most animals but often less so for plants, which may be clonal and  
226 spread vegetatively; a hint of reductionism may already be seen in abstracting individual grass plants  
227 from a meadow, for example. Then, given a method of enumerating individuals, population sizes can  
228 be abstracted by applying the biological species concept (Mayr 1942). This too may be fraught with  
229 conceptual challenges, but armed with a working definition and search-image of a species of

230 interest, an experienced ecologist can assess the numbers of individuals within a specified region  
231 (classically populations are considered as closed to migration). Dividing such counts by the area or  
232 volume of the region then yields population densities, which are the focal quantity in population-  
233 ecology studies. Such densities may be compared over time or space and mathematically related to  
234 each other.

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

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

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



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

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

270

271 [Figure 2 about here]

272

### 273 *The macroecology paradigm*

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

288 The macroecology paradigm has been highly successful in generating laws relating its own  
289 fundamental quantities to each other. While the laws are typically weak, having at least one free  
290 parameter to be tuned to fit empirical data, typical ranges of some parameters have been  
291 characterised, increasing the scope for making predictions. For example, species–area relationships  
292 typically follow a power-law with exponent between 0.15 and 0.4, for plants as well as animals – the  
293 lower end of this range being typical for islands, smaller organisms and higher latitudes (Drakare,  
294 Lennon, and Hillebrand 2006). A contemporary statement of the paradigm's success may be seen in  
295 the celebration of unified theories of biodiversity (McGill 2010). Here Brian McGill focuses on

296 mathematically unifying six theories that each ‘unify ideas of area, abundance and [species]  
297 richness’. But because the latter is commonly presented as ‘biodiversity’, the paper might be naively  
298 taken to present *the* unified theory of ecology!

299 Despite its name and fanfare, we might after all question how far the macroecology paradigm is  
300 intrinsically ecological. Its focus on spatial and numerical abstraction (Caswell 1976) is such that its  
301 laws are not necessarily specific to living organisms: they might equally well describe spatial patterns  
302 of types of non-living artefacts, or in human cultural systems (e.g. Bentley, Hahn, and Shennan 2004)  
303 – and indeed a proportion of its significant papers are published in physics journals (e.g. Blythe and  
304 McKane 2007). While proponents of the paradigm may see this as a mark of success, this must be  
305 tempered by the limited kinds of quantities that can be predicted – which are mostly numerical and  
306 spatial. A similar charge may be laid to the population paradigm: its predictive quantities are  
307 essentially counts of things (individuals, species or occupied patches), and some of its laws might  
308 conceivably apply to non-biotic entities such as molecules in chemical reactions (e.g. Sadownik et al.  
309 2016).

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

315

### 316 *The ecosystemic paradigm*

317 The ecosystemic paradigm originates with the project by Tansley (1935) to use concepts from  
318 physics to understand ecological processes. As such, it defines the *ecosystem* to include non-living  
319 features along with the biotic. This *abiotic environment* is, of course, biotically referenced; it  
320 concerns those physical features that are known (or hypothesised) to affect living organisms, such as  
321 temperature, light and chemicals with which living tissues may interact. This paradigm can also  
322 absorb the ambiguity over whether morbose or detached tissues are living or not (Lindeman 1942).  
323 Integrating living and non-living elements for scientific analysis entails a focus on the highest  
324 common mode of functioning shared by these elements, which is physical. Thus quantities routinely  
325 abstracted in the ecosystemic paradigm include biomass, carbon pools, chemical concentrations,  
326 energy flux rates, evaporation rates and temperature. Such quantities are attributed to ecosystems  
327 and specified compartments within them, although in practice this is often done by drawing upon

328 data attributed to individual organisms and species. The aim is to abstract to a level beyond the  
329 complexities of interactions between specific individuals in order to assess emergent behaviours and  
330 attributes. These typically include such complex concepts as net primary productivity,  
331 evapotranspiration, rates of nutrient cycling and food-web complexity.

332 Candidate laws connecting ecosystem variables are not difficult to find insofar as empirical  
333 relationships are regularly quantified in ecosystem studies. Their predictive power is rarely  
334 impressive, however (Reichstein et al. 2014). The ecosystemic paradigm presents challenges for  
335 ecologists in search of laws more than any other paradigm: its variables are difficult to measure and  
336 highly sensitive to scale, its entities are difficult to observe and define, and the conditions that might  
337 need to be specified as provisos can rarely be controlled or found in steady states. Weak laws have,  
338 nevertheless, been formulated relating ecosystems' productivity, disturbance and diversity, as well  
339 as relationships of these variables to soil nutrient concentrations and rainfall. Examples include  
340 resource response models such as the equations relating overall chlorophyll concentration, plankton  
341 biomass or primary productivity to the total phosphorus concentration of a lake (Table 10.1 in Peters  
342 1991), the intermediate disturbance hypothesis, which states that the species richness of a site will  
343 be maximised at intermediate intensities of disturbance (Wilkinson 1999), and the productivity–fire  
344 relationship, stating that fire intensities are greatest at intermediate levels of habitat productivity  
345 (Reich et al. 2001). Such laws have mostly been arrived at heuristically, through empirical  
346 observation of variables of interest at a range of spatial and temporal scales, followed by statistical  
347 parameterisation.

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

350

### 351 *The trait paradigm*

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

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

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

391 It is true that this statistical–empirical approach could be pursued to the point where a ‘law’ is  
392 discovered every time a statistical model is fitted to data from a broad enough data set (Peters  
393 1991), and some rates of decline in accuracy with increasing scope may be too precipitous to be

394 acceptable. The following is an example of a more theory-driven case – which also brings the  
395 possibility of pre-specifying the kinds of conditions in which a law should most clearly be observed.  
396 The fact that metabolic rates tend to scale as a function of body-size raised to the power of about  
397 three-quarters ( $B^{0.75}$ ), for of all kinds of organisms, had been known for a long time without a  
398 satisfying explanation (Feldman and McMahon 1983) until West, Brown, and Enquist (1997)  
399 published a metabolic scaling theory that explains this relationship in terms of the physics of fluid  
400 flow. Indeed, their theory also predicts observed body-size dependencies for rates of cellular  
401 metabolism, heartbeat and maximal population growth (all  $B^{-1/4}$ ), and time periods of blood  
402 circulation, embryonic growth and life-span (all  $B^{1/4}$ ) (West, Brown, and Enquist 1997). Various other  
403 physiological laws might also be cited here (Peters 1991, 281).

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

411

412

### 413 **MODES OF ANALYSIS AND ASPECTS OF REALITY**

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

426

427 [Table 1 about here]

428

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

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

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

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

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

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

508 Likening a complex situation to something more familiar is the basis of many a scientific  
509 explanation, as suggested by the predominance of metaphors in scientific terminology. Ecology is  
510 replete with these: populations and their carrying capacities; communities, assemblages and  
511 systems; competition, stress and disturbance; and traits and their filters are just some prominent  
512 examples. The analogies behind these metaphors sometimes suggest causal analogues that may be  
513 influential in theorising about a topic. *Carrying capacities* suggest volumes of containers that can  
514 hold certain numbers of items and spill if over-filled – and so the law of density-dependence may  
515 gain a mechanical connotation that seems, to most ecologists (let alone laypersons), to provide a  
516 more compelling causal analogue than any notion of causation acquired from watching the births,  
517 struggles and deaths of moths or fruit flies in jars of medium. *Trait filters* suggest a sieving process  
518 (sometimes directly illustrated – e.g. Keddy 1992) in which certain trait values are admitted to a  
519 collection while others are excluded – and so laws of community composition similarly gain a  
520 mechanical connotation that provides a compelling causal analogue. Indeed, most of the above  
521 metaphors concern mechanical analogies, which prompts the question whether ecologists'  
522 conceptual models are predominantly physical (competition may be the exception in the above list)  
523 – and if so, why. A detailed study of the diversity of conceptual models in ecology and their  
524 relationships to ecological laws would no doubt be illuminating. For now, we may surmise that the  
525 predominance of mechanical metaphors and imagery in conceptual models makes up for the  
526 relatively small contribution of the physical (ecosystemic) paradigm to ecology's laws. Thus, as



527 modes of explanation, the paradigms must complement to each other if one is not to displace the  
528 others.

529

### 530 **A TRULY HOLISTIC ECOLOGY**

531 Contemporary ecological science employs a range of levels of abstraction – manifested in both its  
532 analytical laws and its conceptual models – and analyses phenomena at a range of scales. Our vision  
533 for ecology as a holistic science, then, may be grounded in three features. First, ecology gradually  
534 refines its focus to appropriately-broad spatial and temporal scales of analysis within each of its  
535 paradigms. This is perhaps comparable with the inclusion into physics of such concepts as action at a  
536 distance and statistical mechanics. Second, a portion of its theory (and laws) is based on abstractions  
537 that can only be made of living things. This means not only abstraction of biological classes (common  
538 to all the paradigms), but also of essentially biological quantities such as demographic rates,  
539 speciation rates and trait values. More generally, we might say that ecology sometimes employs the  
540 least reductionistic mode of analysis consistent with its subject matter – and in this sense  
541 contemporary physics, with its understanding of energy, is also more holistic than Newtonian  
542 physics. Thirdly, it is significant that ecology accommodates a range of complementary modes of  
543 analysis, focusing on what may be conceived of as the numerical, spatial and physical aspects of  
544 reality as well as the biotic. It has been claimed that community ecology could be logically and  
545 mathematically reduced to population ecology, and that in turn to ‘individual ecology’ (Schoener  
546 1986), and this may be plausible within areas of those three programmes concerned with  
547 abstraction at the ‘mechanistic’ (*physical?*) level; indeed the claim appears trivial if considered  
548 merely at the spatial level (since the macroecology paradigm can well work with neutral species).  
549 But a claim that the trait, ecosystemic, spatial and population paradigms might be mutually  
550 reducible cannot even be entertained, we suggest, without denying the fundamental concepts of  
551 organisms, flows, patterns and counts as we intuit them. These concepts are not differentiated  
552 simply by scaling, as sometimes claimed; they are logically incommensurable (Clouser 2005, 192f).  
553 This view of ecology’s holism may now suggest some ways in which the versatility and usefulness of  
554 the science may be enhanced by balancing different research paradigms under such a vision.

555 Our view may be summarised by three distinctive proposals. Firstly, ecology can and should have  
556 its own laws, and these may be discovered quite heuristically. Quantitative relationships among  
557 variables abstracted at appropriate levels and measured at appropriate scales are legitimate  
558 candidates for laws of ecology, and the community will determine which ones are sufficiently robust  
559 to be accepted as such. Secondly, our four modes of ecology offer a robust alternative to the typical

560 major divisions of ecology textbooks. Textbooks commonly distinguish population, community and  
561 ecosystem ecology, treating macroecology (if at all) with evolution and trait ecology rather  
562 haphazardly; one of the most popular textbooks reveals a particularly individual-focused emphasis in  
563 its tripartite division into “Organisms”, “Species interactions” and “Communities and Ecosystems”  
564 (Begon, Townsend, and Harper 2006). Thirdly, our view supports broader philosophical challenges  
565 against both reductive physicalism and holistic vitalism. The notion of physical mechanisms being the  
566 ultimate model of causation leaves ecology as a peripheral and inescapably complicated science  
567 (Colyvan and Ginzburg 2003) where *chance* often has to be invoked as a pseudo-cause (Ulanowicz  
568 2009). Vitalism (or idealist holism: Levins and Lewontin 1980), by contrast, tends to advance non-  
569 deterministic explanations – as in the organismic view of plant communities (Clements 1916, cited in  
570 Keller and Golley 2000). Our view, while agnostic about the locus of causation, expects a wide range  
571 of ecological phenomena to be broadly predictable under suitable analyses.

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

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

591

592

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 595 helpful suggestions.

596

597

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

	<b>Population</b>	<b>Macroecology</b>	<b>Ecosystemic</b>	<b>Trait</b>
<b>Approximate synonyms:</b>	Autecology; Species ecology	Neutral /near-neutral ecology	Process ecology	Comparative ecology; Synecology
<b>Focal abstractions:</b>	Population + Species	Spatial pattern + Species	Process + Community	Functional trait + Individual
<b>Other fundamental concepts:</b>	Life-cycle	Habitat patch	Resource fluxes	Niche; Functional type
<b>Typical laws:</b>	Density-dependence	Species–area relationships	Productivity relationships	Trait relationships
<b>Fundamental questions:</b>	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?
<b>Typical application:</b>	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?
<b>Aspect of analysis:</b>	Numerical	Spatial	Physical	Biotic

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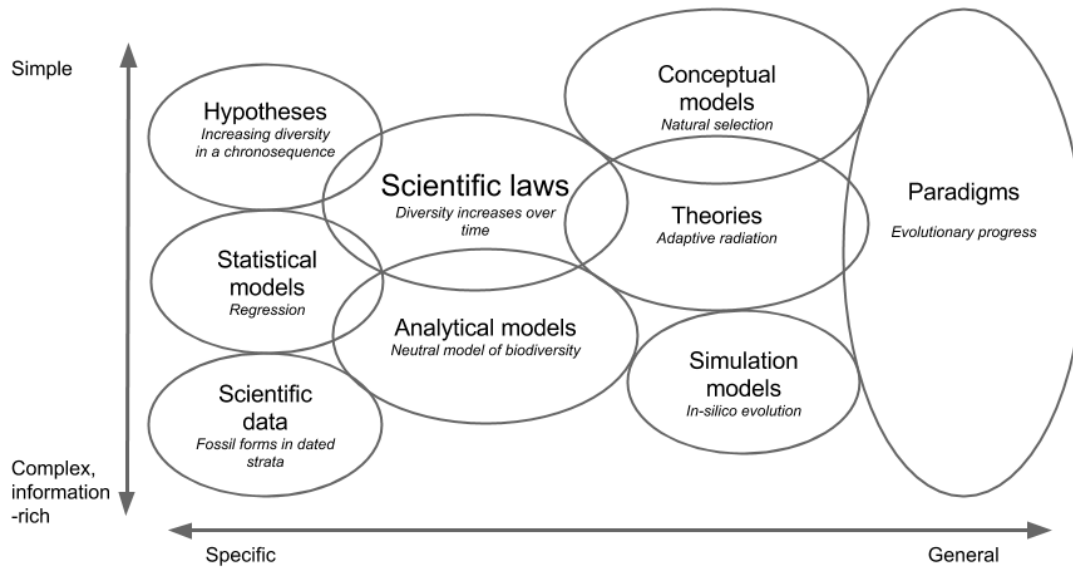
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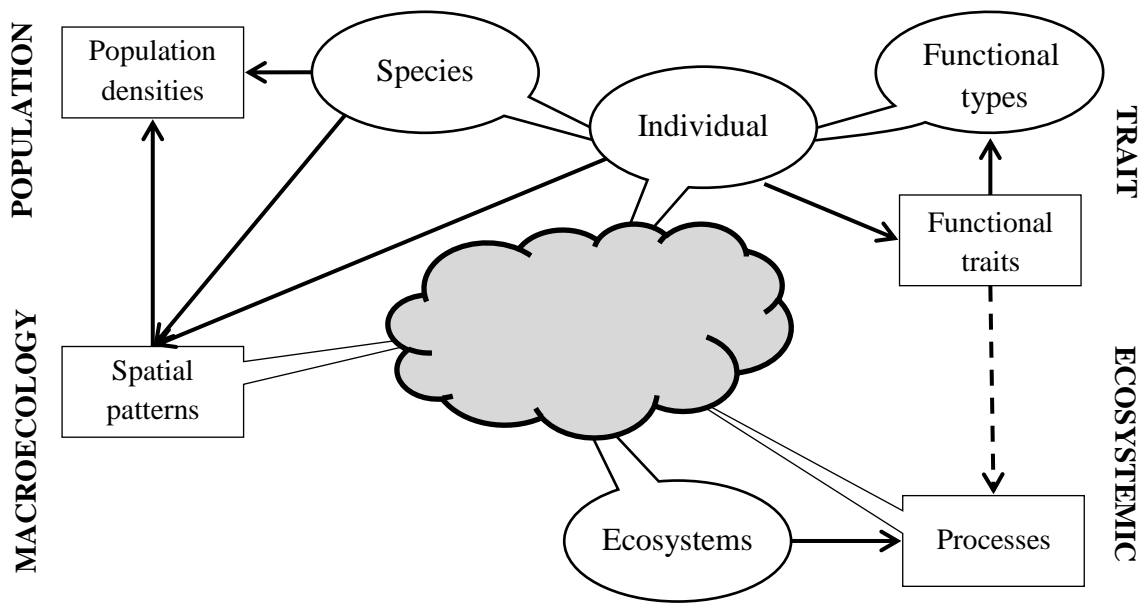


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765 Figure 1. A conceptual map to situate scientific laws among a range of other concepts discussed in  
766 the text. These are ordered from the more specific (left) to the more general (right), and from the  
767 more complex (bottom) to the simpler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



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

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