Acta Biotheor (2011) 59:251–271
DOI 10.1007/s10441-010-9122-9

REGULAR ARTICLE

Causal and Mechanistic Explanations in Ecology

Jani Raerinne

Received: 26 February 2010 / Accepted: 26 November 2010 / Published online: 5 December 2010

Abstract How are scientific explanations possible in ecology, given that there do not appear to be many—if any—ecological laws? To answer this question, I present and defend an account of scientific causal explanation in which ecological generalizations are explanatory if they are invariant rather than lawlike. An invariant generalization continues to hold or be valid under a special change—called an intervention—that changes the value of its variables. According to this account, causes are difference-makers that can be intervened upon to manipulate or control their effects. I apply the account to ecological generalizations to show that invariance under interventions as a criterion of explanatory relevance provides interesting interpretations for the explanatory status of many ecological generalizations. Thus, I argue that there could be causal explanations in ecology by generalizations that are not, in a strict sense, laws. I also address the issue of mechanistic explanations in ecology by arguing that invariance and modularity constitute such explanations.

Keywords Causes · Invariance · Laws · Mechanisms · Modularity · Scientific explanation

1 The Ecological Laws Debate and Accounts of Scientific Explanation

One of the main tasks of philosophers of science is to address how scientific explanations are possible and what is required of such explanations. In the philosophical literature these issues are discussed under "accounts" of scientific explanation, the most famous of which is the covering law account devised by Carl G. Hempel (1965). The covering law account has also been defended by some

J. Raerinne (✉)
Department of Philosophy, History, Culture and Art Studies, University of Helsinki, P.O. Box 24 (Unioninkatu 40 A), 00014 University of Helsinki, Finland
e-mail: Jani.Raerinne@helsinki.fi

ecologists (see Peters 1983: 213–214 and 1991: 148–149; Murray 2000: 406 and 2001: 263–268).

According to the covering law account, a phenomenon is explained by showing that some law covers it as a special case. In other words, phenomena are explained by subsuming them under laws. These ideas apply not only to explanations of particular phenomena or events, but also to explanations of generalizations and laws: the latter are explained or subsumed by other more general laws. The idea of the covering law account is that phenomena are explained when they are shown to happen in accordance with the laws, and therefore these laws should be mentioned in explaining the phenomena. In this sense laws are essential, indispensable, or necessary to scientific explanations. To Hempel, explanations are also arguments in which the conclusion follows either deductively or inductively from the premises.

Since the 1950s, many views, examples, and arguments for and against the existence of biological laws have been presented in the philosophical and biological literature. Recently, ecologists have begun to raise the question of whether distinctive ecological laws exist (see Loehle 1990; Peters 1991; Lawton 1999; Murray 1999, 2000, 2001, 2004; Turchin 2001; Bednekoff 2003; Berryman 2003; Colyvan and Ginzburg 2003; O'Hara 2005; and Owen-Smith 2005).

Although the ecological laws debate is not the topic of this paper, the debate is nevertheless relevant. The reason is that Hempel's covering law account suggests a (historically) influential, practically relevant, and strong justification for this debate, namely, that the proprietary function of laws is to furnish us with scientific explanations. Without justification of such a kind, it is difficult to understand why ecologists are engaged in the laws debate in the first place, given that there do not appear to be many—if any—ecological laws. Thus, the main justification for the laws debate is—or should be—the idea of the covering law account that laws are necessary or indispensable for scientific explanations, a matter that surely is of great interest to ecologists.

Both the validity of Hempel's covering law account and its applicability to the biological sciences can been questioned. There are many counterexamples to and difficulties with this account (see Kitcher 1989: 411–414; Salmon 1984: 28–32, 1989: 46–60, 68–80; and Psillos 2002: 215–262), and it is far from being a settled issue whether ecology has laws of its own (see Raerinne 2010: Chapter 2). I defend an alternative account of explanation in these pages, originally proposed by James Woodward. I will call this account the interventionist account of causal explanation.[1] I defend and develop the account further with ecology in mind. If the interventionist account can be defended successfully, then it would follow that there is no strong, practically relevant, or (historically) influential justification for the

[1] The account is also called the manipulationist account, although interventionist account is a better name for it. The term manipulation seems to be associated with the idea that there is an agent carrying out the intervention. However, any process that fulfills the criteria discussed in Sect. 2 counts as an intervention, regardless of whether it is based on the agency or the activities of humans. For instance, there are natural experiments in which the interventions are those of nature, not of experimenters. In other words, "intervention" is not only broader in scope as a term than "manipulation," but also it is a more accurate term. Finally, with the name "interventionist," I want to distance Woodward's non-reductive account of causal explanation from reductive accounts of causation that are called manipulationist accounts.

ecological laws debate, because laws are neither indispensable nor necessary for scientific explanations. This suggests that the recent debate about ecological laws is a red herring, at least in the context of causal explanations.

I proceed as follows: I first present the interventionist account of causal scientific explanation according to which it is invariance rather than lawlikeness that furnishes generalizations with their explanatory power. I then apply the account to ecological generalizations to show that invariance under interventions as a criterion of explanatory relevance yields interesting and perhaps even unexpected interpretations of the explanatory status of many ecological generalizations, such as allometries, scaling laws, and the species-area rule. Ecologists should find this section interesting, because most of them rely only on unreliable and implicit intuitions, when deciding by what criteria the explanatory status of ecological generalizations should be evaluated. In Sect. 4, I distinguish between two kinds of causal explanations that I call simple causal claims and mechanistic explanations. I also review some recent definitions of mechanisms and argue that (representations of) mechanisms should be defined as invariant and modular. Section 5 concludes.

2 The Interventionist Account of Causal Scientific Explanation

The main claim of this section is that invariance is the correct relation of explanatory relevance in the case of causal explanations, as has been forcefully argued by James Woodward (2000, 2001, 2003a, b; see also Woodward and Hitchcock 2003 and Hitchcock and Woodward 2003), whose ideas I present in this section. The interventionist account to be defended is a realist account of scientific explanations as well. Although explanations can be reconstructed as arguments, explanations are not explanatory as a result of their argumentative structure as they are, for instance, in Carl G. Hempel's (1965) covering law account. Rather, explanations are descriptions of objective dependency relations between things. And the real and independently existing dependency relations of the world determine whether an explanation is true or not. Explanations are explanatory and true if explanations correctly describe dependency relations.

An invariant generalization is one that continues to hold under a special change—called an intervention—that changes the value of its variables. For variable X to be explanatory with regard to variable Y, an invariant relation between the two is required in which interventions of the value of variable X change the value (or the probability distribution) of variable Y in accordance with the relation between the two variables. In other words, what is needed for explanations are interventions or manipulations of generalizations in the form, "if the value of the variable X of a generalization $Y_i = f(X_i)$ were changed by an intervention from x_1 to x_2, then the value of the variable Y would be changed from y_1 to y_2 in accordance with the relation $Y_i = f(X_i)$." The "stability" of a generalization under interventions in its variables is what matters in explanations. For instance, the ideal gas law states that at constant temperature, T, the pressure, P, of gas is inversely proportional to its volume, V, according to the equation $PV = rT$, where r is a constant. The ideal gas law describes how changes in the pressure, volume, and temperature of gases depend on one another and how an intervention in one of the variables brings out changes in the others. In other words, the ideal gas law describes an invariant generalization.

An intervention is a manipulation affecting the value of Y *by changing the value of* X. It should not affect Y via a route failing to go through X. Nor should the intervention be correlated with the other causes of Y, except for those intermediate causes of Y—if there are such—that are between X and Y. As long as a process has the above properties, it is an intervention, regardless of whether it is based on the agency or activities of humans (for a more detailed account of interventions, see Woodward 2000: 199–204, 2003a: 94–111).

An invariant generalization describes what would happen to a value of a variable of a generalization if—perhaps contrary to the fact—a value of one or more of its other variables were changed by an intervention or manipulation:

> [T]he underlying idea of my account of causal explanation: we are in a position to explain when we have information that is relevant to manipulating, controlling, or changing nature, in an "in principle" manner of manipulation…. We have at least the beginnings of an explanation when we have identified factors or conditions such that manipulations or changes in those factors or conditions will produce changes in the outcome being explained. Descriptive knowledge, by contrast, is knowledge that, although it may provide a basis for prediction, classification, or more or less unified representation or systematization, does not provide information potentially relevant to manipulation. (Woodward 2003a: 9–10.)

In order for there to be an intervention and a possibility of a manipulation, at least some of the predicate terms of a generalization are required to be (representable as) variables (see Woodward 2000: 206–209, 2003a: 111–114). If there is no well-defined notion or idea of what it would mean to change a value(s) of a predicate term(s) of a generalization, or what it means to represent its predicate terms as variables, then the generalization is not invariant. Woodward calls such generalizations *non-change-relating*. The idea is that non-change-relating generalizations do not describe "dynamic" relations. Generalizations expressing static, qualitative, or categorical relations can often be viewed as non-change-relating.

Consider a generalization that is sometimes presented as a physical law, owing to its high degree of stability: "all noble gases are chemically inert." Although this generalization is stable in the sense that it holds in many different background conditions, it is not invariant, because it does not allow for a (well-defined) change in its predicate terms, "noble gases" and "chemically inert." In fact, the generalization denies any changes in the properties of noble gases that could be used in the manipulation of their properties. A necessary (although not sufficient) condition for a generalization to count as explanatory and invariant is that it expresses a *change-relating* generalization (see Woodward 2003a: 245–254). Although invariant generalizations are change-relating, not all change-relating generalizations are invariant.

Invariance is a degree concept with a threshold (see Woodward 2000: 214–222, 2003a: 257–265). There are generalizations that are not at all invariant, such as the above example of noble gases. Likewise, there are change-relating generalizations, such as correlations between factors that are joint effects of a common cause (i.e., confounding factors or cases of spurious causation), which are not invariant. A non-invariant, but change-relating relation between joint effects of a common cause breaks down during interventions in its effects. An example is the correlation between readings on a barometer and the occurrence of storms that correlate owing to their common cause, namely, the changes in atmospheric pressure: changing the value of one effect (a reading on a barometer) does not make any difference to the value of another effect (the occurrence of storms), although the correlation between the two can be very stable in the sense that it holds in many different background conditions. In other words, joint effects of common causes express change-relating generalizations that fail to be invariant during interventions. Only interventions in the value of a common cause make a difference to the values of the joint effects correlating.

Above the threshold of invariance there are more or less invariant generalizations. Woodward calls the invariance domain the set or range of changes over which a generalization is invariant (see Woodward 2000: 205–209, 2003a: 239–314). This range need not be universal in the sense that during all the interventions on its variables, a generalization holds. A generalization remains invariant and explanatory even if during some interventions, it breaks down. Typically, generalizations fail to be invariant under extreme values of their variables and/or under some background conditions. The ideal gas law, for instance, breaks down under extreme pressure. Thus, generalizations can be explanatory with exceptions and even if they hold true only in special background conditions.

Explanations describe and exhibit how the phenomena-to-be-explained systematically depend upon the changes of things that do the explaining. Invariant generalizations provide answers to “what-if-things-had-been-different” questions that provide us with understanding and explanatory information about how the phenomenon-to-be-explained would have changed had we changed the initial or boundary conditions of an invariant generalization to “such-and-such” (see Woodward 2000: 209–214, 2003a: 187–194, 196–203).

There is a connection between invariance domain and explanatory depth (see Hitchcock and Woodward 2003). The ideal gas law and van der Waal’s force law both describe how changes in the pressure, volume, and temperature of gases depend on one another and how an intervention in one of the variables brings out changes in the others. However, van der Waal’s force law has a larger invariance domain than the ideal gas law, since it holds in conditions in which the ideal gas law breaks down, such as under extreme pressure. Consequently, it could be suggested that van der Waal’s force law provides deeper explanations about the behavior of gases than do the ideal gas laws, because van der Waal’s force law answers more of the “what-if-things-had-been-different” questions, owing to its larger invariance domain.

As the above suggests, sometimes the invariance domain of a generalization is a proper subset of the invariance domain of another generalization. In such cases it is straightforward to claim that the latter generalization provides deeper explanations of their common object of an explanation than the former, because the latter answers more of the "what-if-things-had-been-different" questions about that particular object of an explanation. Nevertheless, such cases are possibly the exception rather than the rule; it is likely that invariance domains of many *explanantia* only intersect, which makes it more difficult to estimate which of the *explanantia* provides deeper explanations of their object of an explanation than other(s). Moreover, it is both the nature and the range of interventions that determine how shallow or deep are the generalizations of explanations offered (see Woodward 2000: 220–222, 2003a: 257–265). This is because certain interventions are considered privileged or more important than others in different sciences or disciplines in the sense that generalizations should remain invariant under them. Let me therefore suggest that one generalization provides deeper explanations than another of their common object of an explanation if it remains invariant under a wider and/or more important set or range of interventions. However, whether a generalization (or regularity) remains invariant during interventions is an objective fact that is unaffected by the considerations of importance we attach to interventions. For discussion of other dimensions of explanatory depth between different explanations of an object of an explanation, such as precision and factual accuracy, see Petri Ylikoski and Jaakko Kuorikoski (2010).

Invariance is different from stability (see Woodward 2001: 13–17, 2003a: 295–302, 2006, 2010; see also Mitchell 1997, 2000, 2002). Call a generalization stable if it holds in many possible background conditions. For instance, the generalization "all persisting lumps of pure uranium-235 have a mass less than 1,000 kg" appears stable, because it depends on a small number of nuclear physical facts that are pervasive and deep facts about the universe. Unstable generalizations require a host of incidental conditions to remain true or to hold. For instance, the generalization "all persisting lumps of pure gold have a mass less than 1,000 kg" holds true only because several incidental background conditions are in place. In other words, it is a coincidence that nobody has amassed gold into a lump weighing over 1,000 kg, although nothing precludes that such an event should not be true. Yet physical laws, namely, the laws of nuclear chain-reactions, bar of existing a lump of uranium isotope 235 with a mass of 1,000 kg, because this is much greater than the critical mass of the isotope, which is around 50 kg, depending on the shape and density of the lump. Stability is a matter of degree as well: a generalization is more stable the more possible background conditions there are in which it holds.[2]

There are stable generalizations that are not invariant. For instance, change-relating correlations between joint effects of a common cause can be stable in the sense that they hold in different background conditions. These, nevertheless, are non-invariant as generalizations. Although it is invariance—rather than stability—that furnishes us with explanatory generalizations, there is an important function that stability has in the context of explanations, namely, stability furnishes us with *extrapolability and reliability* of explanations (cf. Mitchell 1997, 2002; Woodward

[2] Of course, stability does not depend only on the number, but likewise on the nature of the background conditions. There are background conditions to which some generalizations (or rather regularities) are very sensitive to in their holding, whereas other conditions have milder impacts on their holding. Likewise, in certain sciences and disciplines certain background conditions are deemed as more important than others.

2006, 2010; and Raerinne 2010: Chapter 5). In general, the larger the stability domain of a generalization, the more extrapolable and reliable the generalization is, because it holds in many—and/or in more important—different possible background conditions rather than holding owing to some actual or incidental background conditions. A lack of stability of a generalization has the effect of diminishing its extrapolability and reliability.

Invariance is also different from generalizations' lawlikeness (see Woodward 2000: 222–228, 2003a: 265–272). There is no requirement that invariant generalizations should contain only purely qualitative predicate terms, be universal, maximally or highly stable, or belong to a systematic web of other generalizations, as many philosophers have suggested about laws (see Hempel and Oppenheim 1948: 152–157; Nagel 1961: 47–78; Lewis 1973; and Lange 2005). A generalization can be invariant and explanatory regardless of its lawlike status.

The interventionist account has many advantageous features. It resolves the problems of explanatory irrelevance and asymmetry, which have plagued previous accounts of scientific explanation (see Woodward 2003a: 196–203). The account allows for explanations of phenomena that have low probabilities of occurrence in contrast to some other accounts. Untreated syphilis is the cause of and can be used to explain the development of paresis, although only a small percentage of syphilitics develop paresis. This is because the incidence of paresis is higher among syphilitics who have not been treated than among those who have been. For a variable to count as an indeterministic cause of an effect, it is not required that it raise (or lower) the probability of the occurrence of its effect in every background condition, only that the variable should do this under some of the interventions in some background conditions (see Woodward 2003a: 147–149). This last feature is especially fortunate, since many ecological generalizations seem to lack stable probabilities, and many ecological causes evidently are not unanimous in their effects. The interventionist account thus gives normatively right answers to many issues about explanations. This much cannot be said about any other account of scientific explanation.

3 Ecological Generalizations

Invariance under interventions as a criterion of explanatory relevance gives interesting and even unexpected interpretations of the explanatory status of many ecological generalizations. According to the interventionist account, many (large-scale) ecological generalizations are *not* explanatory, because they do not describe invariant relations. Putative examples include the *intra*specific and *inter*specific patterns of abundance and distribution, the canonical distribution of abundances, and the hollow curve, which represents phenomena-to-be-explained or "patterns" rather than things that do the explaining.[3] This is because the above generalizations

[3] According to the *intra*specific pattern of abundance and distribution, abundance is highest at the center of each species' range and declines gradually and usually symmetrically toward the boundaries. According to the *inter*specific pattern of abundance and distribution, the abundant species tend to be widely distributed, while the rare species tend to have restricted ranges. The canonical distribution of

are either non-change-relating or change-relating, but not invariant during interventions. This is *despite* the fact that many of the above generalizations could be stable generalizations, owing to their validity or holding in many different background conditions.

Why do I claim that these generalizations are not explanatory? Well, it appears to be difficult to determine exactly what variables should be manipulated in these generalizations and exactly what kinds of effects the manipulation of "explanatory" or independent variables should have on other variables mentioned in these generalizations. This suggests that the generalizations are *non*-change-relating. However, even if there were a well-defined notion of what is to be manipulated and of the results of such manipulation, I suppose that many of the above generalizations would break down during interventions. Thus, even if these generalizations represented stable and change-relating generalizations, they are likely to be only joint effects correlating, owing to their common causes, that is, cases of spurious causation, rather than invariant generalizations.

The interventionist account gives experimentation and manipulation a central place in establishing and testing explanatory generalizations. The interventionist account seems to accord well with the intuitions and practices of many ecologists concerning explanation and experimentation (cf., for instance, Hairston 1989). Nevertheless, some biologists use non-manipulative and non-experimental methods, such as regression equations and other correlations, to study phenomena. These are widely used in ecology and paleobiology, for instance, under the rubric of "allometries and scaling laws."

Allometries and scaling laws are regression equations represented as power equations in which one variable changes as a power of another. These take the form

$$Y = aW^b,$$

where Y is the dependent variable (or response), W represents the independent (or "explanatory") variable, a is the normalization constant, and b is the scaling exponent.[4] In allometries and scaling laws body size or weight is treated as an independent variable of anatomical, physiological, morphological, behavioral, life historical, ecological, or paleobiological traits of taxa (see Newell 1949; Rensch 1960; Gould 1966; Clutton-Brock and Harvey 1983; Peters 1983; McKinney 1990; Brown 1995: especially 76–101; Marquet 2000; Marquet et al. 2005).

Footnote 3 continued
abundances of species (also known as the approximately lognormal distribution of abundances of coexisting species, the canonical distribution of commonness and rarity, the distribution of abundance among species, and Preston's lognormal distribution) claims that there are more moderately rare species than moderately common ones. In other words, ecological communities contain many relatively rare species and only a few very abundant ones. Finally, according to the hollow curve (also known as the distribution of range sizes among species), there is a right-skewed species range size distribution, that is, most species have moderate to small range sizes and only a few have large range sizes.

[4] I have omitted error terms that represent variation in the dependent variable, owing to other possible independent variables and measurement errors in the independent variable.

Depending on the value of their scaling exponents, allometries and scaling laws are called either allometric ($b \neq 1$) or isometric ($b = 1$). Scaling exponents can take both negative and positive values. In general, the larger the value of b, the faster Y increases (if b is positive in value) or decreases (if b is negative in value) with increasing W. If the scaling exponent, b, is less than unity, then Y increases (or decreases if negative in value) more slowly than W. After logarithmic transformation the above equations become linear and yield straight lines on double log axes, where a gives the intercept or elevation of the regression line and b, its slope.

There is a plenitude of biological traits that correlate with body size, W, and can be represented as dependent variables, Y. Robert Henry Peters (1983) has provided hundreds of examples of allometries and scaling laws. Some of the more common are the following:

1. Energy use is unaffected by body size: according to the energy equivalence rule, the energy use of all species (populations) in each size class tends to be equal, scales as aW^0
2. Fasting endurance scales as $aW^{0.44}$ for mammals and between $aW^{0.40}$ and $aW^{0.60}$ in birds
3. The size of the home range of birds and mammals varies positively with body size, aW^1
4. The inverse scaling rule: the maximum density, D, of herbivorous mammals declines as their body size increases, $D = aW^{-0.75}$
5. Kleiber's rule: basal metabolism, an estimate of the energy required by an individual for the basic processes of living, varies as $aW^{0.75}$
6. An Individual's total energy consumption varies as $aW^{0.75}$
7. In most mammal groups gut volume is isometric to W, aW^1
8. Heart rate varies as $aW^{-0.25}$
9. In mammals within species sociality increases with body size
10. Group behavior increases with body size in mammals

Even though we know that correlation is not intimately or necessarily connected to causation, in practical terms this dictum is sometimes forgotten in the literature on allometries and scaling laws. In this literature, body size as an independent variable is sometimes claimed to explain (a major) part of the variation in the dependent variable. How much it explains is dependent on the indices of fit, e.g., on the value of r^2. According to the interventionist account defended, however, correlations by themselves are not explanatory, regardless of how strong and/or stable the connection between the correlating factors is. For a correlation to be explanatory there has to be an intervention during which the relation between factors remains invariant.

Below are some general reasons to be suspicious of explanatory and causal relevance of *some* allometries and scaling laws. There are other problems with these regression equations that I will not take up here. For instance, I do not discuss the statistical problems and the problems of fitting data to regressions that are relevant in interpreting allometries and scaling laws and that affect their reliability (see Gould 1966; Peters 1983: 10–23; McKinney 1990). Nor do I discuss the adaptive significance of allometries and scaling laws (see Rensch 1960; Bonner 1968; and

Clutton-Brock and Harvey 1983). Finally, I have discussed the lawlike status of allometries and scaling laws elsewhere (Raerinne 2010).[5]

In many cases "body size" is used as an independent variable, owing to convenience. Body size is relatively easy to quantify, compare, and estimate from fossil parts and other field samples. As a result of its convenient features, body size is often not intended to be a cause variable, but a proxy for or a correlate of other features that are not so easy to quantify, compare, or estimate and which represent the real causes. This becomes a problem if body size is subsequently interpreted to be the cause variable. It is problematic because using body size in this manner is not only causally inaccurate and false, but also misleading insofar as we are searching for ways to intervene in nature. Another problem arises when the use of body size as a proxy hides the fact that the real causes of allometries and scaling laws are not well defined as variables (see below).

A necessary condition for a generalization to count as invariant is that it expresses a change-relating generalization. The problem in this context is that sometimes it is not easy to understand how some allometries and scaling laws represent change-relating generalizations. Sometimes the *dependent* variable in allometries and scaling laws is such that it is difficult to understand what it means to change its value and/or what its different values would be. In other words, the problem is how dependent variables are to be represented as variables that have well-defined values. Consider, for instance, the two regressions presented above that relate body size to "within species sociality" and "group behavior." These generalizations are possibly non-change relating, because what is meant by "within species sociality" or "group behavior" as variables appears not be well defined. If this is true, then it follows that it is unclear how changes in the value of an independent variable affect the dependent variables, simply owing to the fact that the dependent variables are not well defined. As was just discussed, body size is often used as a proxy for the real causes of dependent variables of allometries and scaling laws that are not so easy to quantify, estimate, and so on. In fact, precisely because the real causes are not well-defined as variables, body size is apparently sometimes used as a proxy. Such use is inappropriate, since it hides the fact that the allometries and scaling laws in question are non-change relating as generalizations.

The interventionist account of scientific causal explanation gives manipulation a central place in establishing that we have a causal or explanatory relation. Furthermore, the real and independently existing dependency relations determine whether we have an explanatory relation or not. Consequently, if a generalization cannot be tested for how it might behave during interventions in or manipulations with its variables, then the claims made about its explanatory status should be treated with suspicion. The unfortunate fact in this context is that testing whether ecological and paleobiological regression equations represent invariant generalizations is often

[5] In particular I have argued against recent views that regard allometries and scaling laws as representing biological laws. Although allometries and scaling laws appear to be generalizations applying to many taxa, they are neither universal nor exceptionless. In fact there appear to be exceptions to all of them. Nor are the constants in allometries and scaling laws truly constant, stable, or universal in character, but vary in value across different taxa and background conditions. Moreover, these equations represent evolutionary contingent generalizations, which threaten their lawlike status.

difficult purely for scale-related reasons (cf. large ecosystems studies and paleobiological allometries and scaling laws) and owing to many ethical, technical, and other reasons.

When the problems above can be avoided, it is quite likely that many allometries and scaling laws turn out to be change-relating but *non*-invariant during interventions. Thus, even though many allometries and scaling laws represent change-relating generalizations, it is quite possible that they might be joint effects correlating, owing to their common causes—that is, accidents that hold because of their common causes. Correlations between factors that are joint effects of a common cause break down during interventions in its effects. Even if we find that some of these generalizations are *change-relating and invariant*, allometries and scaling laws seem to offer rather shallow and superficial explanations—or "simple causal claims"—that need to be supplemented with information about the mechanisms that underlie them.

In principle, I have nothing against the idea that regression equations may be causal or explanatory. Again, whether these relations remain invariant during their interventions is the objective criterion that determines whether they are explanatory or not. It is the naïve use of regressions encountered in the literature that I object to here.

There is, nevertheless, another important function that the regression studies mentioned above have. Many allometries and scaling laws should be understood as *elucidating phenomena from data*—they describe and classify phenomena-to-be-explained rather than things that do the explaining. This function is not to be overlooked. For instance, if the energy equivalency rule is generally true (i.e., it has a large scope and/or is very stable), then it is interesting as an object of explanation that would have other interesting implications. As another example, homeotherms, poikilotherms, and unicellular organisms have different a values in equations that relate their metabolic rates to body size. In the equation for a basal metabolic rate (Kleiber's rule), which scales with body size as $aW^{0.75}$ in these taxa, the values of a are 4.1, 0.14, and 0.018 for homeotherms, poikilotherms, and unicellular organisms (Peters 1983: 29–30). Rather than indicating universal laws and/or explanatory generalizations with immutable constants, these generalizations represent interesting objects of explanation. Why is it that unicellular organisms have the lowest values of a in such equations? How and why do homeotherms metabolize at a higher level (and thus seem to utilize and exhaust relatively more resources) than poikilotherms and unicellular organisms of similar size?

Does the claim that some allometries and scaling laws represent only phenomena-to-be-explained (or *explananda*) rather than things that do the explaining (or *explanantia*) cast a shadow over allometry and scaling law studies? No. A science or discipline without interesting *explananda* lacks the potential to progress and mature. In this respect these studies show a great potential.

It is easy to criticize the ideas presented above by suggesting that there is a "mathematical sense" of explanation according to which allometries and scaling laws are explanatory, regardless of their explanatory status in the context of causal explanation, as has been suggested to me. One problem with this suggestion is that it is difficult to explicate what this mathematical sense of explanation consists in or to develop this sense into a full-blown account of mathematical explanation (see, for instance, Sandborg 1998 and Mancosu 2008). There is one account of scientific explanation that perhaps could used, namely, the unification account by Philip Kitcher (1989). But Kitcher's account has faced serious difficulties in the context of non-mathematical explanations, which suggests that it is defective as a general account of scientific explanation. Nor has the unification account been properly applied to mathematics to determine how well it accounts for the mathematical sense of explanation. In other words, the "mathematical sense" of explanation rests on undeveloped ideas and (unreliable) intuitions. Moreover, the idea of a mathematical sense of explanations is evidently not first and foremost to show how regression equations could be explanatory "in the non-causal sense of the word," but rather to explain how and under which conditions such mathematical activities could be explanatory as providing proofs and solving equations. Finally, allometries and scaling laws should be dealt with in the context of causal explanations, since the authors who discuss them interpret allometries and scaling laws to be about the causal relations between body size and the dependent variables mentioned in them. I have nothing against the idea that there should be mathematical explanations that differ from causal explanations. Another paper would be needed to explore the legitimacy of this account fully.

As another example, consider the species-area rule. According to this rule, the number of species (on an island) varies with the area (of that island), where this relation can be presented as a power equation, $S = cA^z$, in which S is the number of species of a given taxonomic group, A is the area (of the island), and c and z are (fitted) constants. There appears to be an invariant relation between the variables area and species diversity (see Simberloff 1976) despite the fact that the mechanism(s) behind the rule are disputed (see Preston 1962; Simberloff 1974, 1976; Diamond 1975; Connor and McCoy 1979; Gilbert 1980; Williamson 1989; Lawton 1996). According to a rule of thumb, the manipulation of an area of an island or habitat that ten-fold it, doubles the species diversity. The explanatory status of the species-area rule does not depend on there being a generalization that is universally true that holds in many or most background conditions, and that has no exceptions (see Cook 1974; Gilbert 1980). In other words, it does not depend on the putative lawlike status of this rule as some authors believe (see Simberloff 1974; Lawton 1996, 1999; Lange 2005). Rather it depends on whether the rule is invariant during its interventions or not.

Some other putative examples of invariant ecological generalizations include the area rule of the equilibrium theory of island biogeography, the distance rule of the equilibrium theory of island biogeography, the diversity-stability rule, the endemicity rule of the equilibrium theory of island biogeography, and the intermediate disturbance rule. According to the area rule, an island's extinction or turnover rates depend on the island's size. When an area of an island is decreased (or increased), its species extinction rate is increased (or decreased). According to the distance rule, the immigration rates of islands depend on their distance from the continental source of the immigrant species. When the degree of isolation from the source region(s) of an island is increased (or decreased), its immigration rate is reduced (or increased). According to the diversity-stability rule (also known as the complexity-stability rule), increased (alpha, beta, and/or gamma), diversity enhances (population, community, and/or ecosystem) stability.

As a final example, I will show how the intermediate disturbance rule could represent an invariant generalization. In (rocky) intertidal marine habitats the top predators (e.g., starfish and gastropod species of genera *Thais* and *Pisaster*) prey on different consumer species (the different mussels, barnacles, and other species of many genera). In such habitats, there is severe and intense competition among the consumer species for living space, which is the major and critical limiting factor. However, there is surprisingly high alpha diversity of the consumer species in many such habitats. It is surprisingly high, because, on the basis of Gause's rule, one would expect only a few species, given the keen competition for living space.

What Robert T. Paine (1966) experimentally discovered was that removing one (or more) of the top predator species (e.g., *Pisaster*) from such a habitat had the effect of *reducing* the alpha diversity of the consumer species: without a common predator species, a few (and perhaps even one) competitively dominant consumer species comes to monopolize the living space by outcompeting other consumer species. Thus, (the top or key-stone) predators mediate the coexistence of their prey and maintain the local diversity of a community by keeping competing prey populations' densities or abundances below some level at which the competition would become so severe as to cause local extinctions. Other experiments have reported similar results (see Slobodkin 1964; Paine and Vadas 1969; and Durán and Castilla 1989).

These and similar experimental findings and explanations of exceptions to Gause's rule by Paine and others were later generalized and labelled the intermediate disturbance rule. According to this rule, intermediate levels of abiotic or biotic disturbances, such as predation, pathogens, aridity, storms, and fires are capable of mediating the coexistence of competitor species and thus maintaining the local diversity of a community at a relatively high level. Too small or infrequent disturbances lead to local extinctions of competitively inferior species by competitively dominant ones, whereas too intense or too frequent disturbances allow for the few species that are the most stress-tolerant to exclude other species from a habitat. In other words, local species diversity often peaks with the intermediate levels of disturbances of a habitat. Biotic and abiotic disturbances have the same effect, for instance, through reduction of population densities of competitor species, which counter the strong competitive effects between species.

4 Simple Causal Claims and Mechanistic Explanations

A frequently raised claim is that ecologists explain phenomena or patterns by mechanisms.[6] Yet ecologists have not given us definitions of mechanisms. For them, the concept is evidently pragmatic: mechanisms are things—whatever they are—doing the explaining of phenomena. Ecologists likewise speak of causes and

[6] See, for instance, Brown (1995: 119–187), Gaston (1996), Blackburn et al. (1999: 170–172), and Ashton et al. (2000: 406–410).

processes as something explaining phenomena (or "patterns") without being explicit about what the causes or processes are.

In the interventionist account defended here, causes are difference-makers. One should understand causes and effects as (representable as) variables. Many vernacular causal locutions can be understood to be about binary-valued variables. Causes are difference-makers in that they can be intervened upon to manipulate or control their effects. A change in the value of a cause makes a difference in the value of its effect. Consequently, the species-area rule, for instance, can be called a causal generalization, if it is true that an intervention in an area of a habitat makes a difference in its species diversity. This formulation extends to indeterministic contexts, where causes make a difference in the probability distribution of effects, such as when a drug makes a difference in the probability of the recovery of a patient.

There is a distinction in the philosophical literature between two kinds of causal explanation, which I shall call "simple causal claims" and "mechanistic explanations." A simple causal claim describes the causal connection between the phenomenon-to-be-explained and the thing that does the explaining. It refers to a "phenomenological" or superficial causal explanation in which one has an invariant relation between variables, but no account—or mechanistic explanation—as to why or how the relation holds between the variables.

The account of explanation presented above describes how simple causal claims function by identifying what is required of a causal dependency relation to be explanatory. That is, simple causal claims need to be invariant during interventions. Describing a mechanism of a phenomenon is not something that is contrary to describing what the causal dependency relation of a simple causal claim of that phenomenon is. Instead, a mechanistic explanation is a complement to a simple causal claim, since it describes *how* the dependency relation produces its phenomenon-to-be-explained.

A mechanistic explanation describes the internal causal structure of the phenomenon-to-be-explained. It describes the underlying mechanism *within* the system by showing how the system is constituted and how this produces the phenomenon-to-be-explained. Mechanistic explanations are causal and bottom-up explanations. Next I will address the issue of what mechanistic explanations are by arguing that invariance and modularity are their main elements. Again, mechanistic explanations are causal explanations as a result of their invariance. Mechanistic explanations or representations of them are explanatory and true if they correctly describe the mechanisms in nature.

Recently, interest has revived in mechanisms in the philosophy of science. Previous philosophers had usually considered the concept to be primitive and had failed to define mechanisms (cf. Wimsatt 1976) and/or investigated mechanisms as the physical sciences in mind. For instance, Wesley C. Salmon (1984, 1989, 1994) gave no definition of mechanisms. Moreover, his causal processes interacting, which evidently constituted his mechanisms, were discussed with the physical sciences in mind. And there are serious doubts about whether his ideas concerning causal processes can be extended or applied to the biological sciences. Finally, there are serious difficulties with Salmon's causal-mechanical account of explanation that suggest it is not successful as an account (see Kitcher 1989: 459–477 and Hitchcock 1995). Thus, previous philosophers shed no light on the questions of what mechanisms are in biology or ecology and how they furnish us with explanations or understanding of phenomena there.

Fortunately, there are some recent (non-Salmonian) definitions of mechanisms in the philosophical literature. The most well-known is the one given by Peter Machamer et al. (2000: 3):

> Mechanisms are entities and activities organized such that they are productive of regular change from start or set-up to finish or termination conditions.

I have no doubt that these authors give a more or less accurate *description* of mechanisms at least in such biological disciplines as neurobiology, molecular biology, cytology, and perhaps even ecology (see Pâslaru 2009). However, I have one problem with their definition; namely, they do not tie their definition to any account of scientific explanation that would tell how or under what conditions (descriptions of) mechanisms are explanatory. This makes their definition of mechanisms normatively shallow or unenlightening. This same problem applies to other recent definitions of mechanisms that are, in other respects, different. For instance, it applies to William Bechtel and Adele Abrahamsen's (2005) definition of mechanisms and to Stuart Glennan's (1996).[7]

Thus, the problem is not so much that of giving accurate definitions or descriptions of mechanisms in the biological sciences, but to come with an account of mechanistic explanation. As a solution to the latter problem, I suggest that we adopt James Woodward's definition of (representations of) mechanisms, which ties mechanisms to the account of scientific explanation presented above by emphasizing the modularity of components of mechanisms and invariance as the activity of the components:

> (MECH) a necessary condition for a representation to be an acceptable model of a mechanism is that the representation (i) describe an organized or structured set of parts or components, where (ii) the behavior of each component is described by a generalization that is invariant under interventions, and where (iii) the generalizations governing each component are also independently changeable, and where (iv) the representation allows us to see how, in virtue of (i), (ii) and (iii), the overall output of the mechanism will

[7] Now, it is true that, for instance, Stuart Glennan (2005) and Carl F. Craver (2007: 107–162) have in their more recent and revised definitions of mechanisms, also defended "Woodwardian" definitions of mechanisms as I do below by emphasizing that the behavior of components of mechanisms should be describable by invariant generalizations. However, neither Glennan nor Craver have defended Woodward's modularity condition and neither of them discuss mechanistic explanations in the context of ecology as I do here. However, there is one paper that discusses mechanisms in ecology as well as their modularity, namely, Viorel Pâslaru's (2009). Pâslaru claims that Woodward's definition of mechanisms (to be defended in this section) is not sufficient for ecologists. Instead, he suggests, ecologists seek something similar to the definition of Machamer et al. (2000) as the correct description of their mechanisms. This observation may be correct. However, there is one problem in Pâslaru's paper. Pâslaru also seems to confuse the description or definition of mechanisms (and/or the fact that mechanistic explanations need to be "anchored" in entities, activities, and their organization) with the normative account of mechanistic explanation. The latter is discussed here, not the former.

> vary under manipulation of the input to each component and changes in the components themselves. (Woodward 2002: S375.)

One can think of a representation of a mechanism as a modular system of invariant generalizations or equations. Modularity can be understood to do with "the separability of different causal contributions to an overall effect" (Mitchell 2008: 699). In a modular system it is possible—at least in principle—to intervene in a variable of some generalization or equation without interfering or disturbing *other* generalizations or equations of that system. In other words, a component of a mechanism should be *independently changeable* with its other components (for a detailed presentation of the modularity condition, see Woodward 2003a: 327–342; see also Hausman and Woodward 1999, 2004; Cartwright 2002; Steel 2006).

Physical mechanisms are governed by physical forces. Consider physical component forces of Newtonian theory, such as gravitation and electricity, which have effects on the acceleration of massive bodies. As far as we know, these physical component forces are such that that we can intervene on one of these forces, say, gravitation (as in Newton's law of gravitation) without interfering with other such forces, say, electricity (as in Coulomb's law). In other words, it is possible to intervene on a mass of a system without affecting its charge. Thus, physical component forces are independently changeable or modular. I will assume that many ecological "component forces," such as competition and predation, are modular as well.

If a component of (a representation of) a mechanism is not modular under an intervention, then it is possible that one has misrepresented or mis-decomposed the mechanism into components. Likewise, a non-modular system cannot be used to provide answers to "what-if-things-had-been-different" questions that provide us with understanding and explanatory information about the phenomenon-to-be-explained. The reason for this is that in a non-modular system, interventions are not "surgical" in the sense that they would affect only the intervened-upon component, but they affect other components of the system as well, with unpredictable effects on the system's behavior.

There are counterexamples to the above definition. Some (biological) mechanisms are not modular in any general and/or absolute sense, but are non-modular under some interventions. Nancy Cartwright (2004: 807–811) and Sandra Mitchell (2008) think that this ruins the above definition. However, modularity as a condition should not be understood in an absolute or "either/or" sense, but as a degree condition of components, in contrast to above authors. It is likewise not a condition evaluated in isolation, but in comparison to interventions, for some interventions are more likely to be "structure-altering" than others (see Steel 2008: 154–160 for an interesting general discussion with examples). Thus, it is a mistake to think of modularity as a general, unconditional, and non-relative condition of (representations of) components of mechanisms or to claim that because some (biological) mechanisms are not modular under some interventions, modularity as a condition is questioned.

Examples of mechanisms and mechanistic explanations from philosophers of biology typically come from genetics, molecular biology, and neurobiology. We philosophers seem to be enthusiastic about such paradigmatic examples of mechanisms as photosynthesis (Tabery 2004: 4–8), the Krebs cycle (Perini 2005: 260–265), protein synthesis or the central dogma of molecular biology (Machamer et al. 2000: 18–21; Darden 2002, 2005), cellular respiration or metabolism (Bechtel and Abrahamsen 2005), Mendel's rules and Mendelian genetics (Glennan 2005: 446, Darden 2005), action potentials and synaptic plasticity (Craver 2002: S85–S88 and 2007; Bogen 2005), and the replication of HIV (Steel 2008: 55–58).

Many ecological mechanisms are not well known. In fact, most mechanistic explanations in ecology are undetermined by data or lacking in data (see Pianka 1966, whose paper is representative of ecological mechanistic explanations even today). Thus, many causal explanations in ecology are simple causal claims in the sense that there are no known or confirmed mechanistic explanations, for how the causes in these explanations produce their effects. This is true, for instance, of the species-area rule in which the "area" seems to be a cause of "species diversity," although we do know exactly why or how because the mechanism(s) behind this rule are disputed and under discussion. When ecology is contrasted with other biological disciplines, such as genetics, molecular biology, and neurobiology, in which the mechanistic aspects of explanations seem to be more prominent, ecological causal explanations appear to be "phenomenological" invariant generalizations whose mechanistic aspects remain to be discovered. This is the reason why I am unable to provide the reader with a paradigmatic example of an ecological mechanism or mechanistic explanation (but see also Pâslaru 2009). Yet it is not my task to provide these, but rather it is the task of ecologists. My task was to discuss and defend an account of mechanistic explanation.

5 Conclusions

I have defended an account of scientific explanation. According to it, it is the invariance of generalizations that gives generalizations explanatory power. An invariant generalization continues to hold or be valid under a special change—called an intervention—that changes the value of its variables. A generalization can be invariant and explanatory regardless of its lawlike status. The interventionist account provided interesting and perhaps even unexpected interpretations of the explanatory status of some ecological generalizations. The nature of mechanistic explanations in ecology was likewise discussed.

The interventionist account covers causal explanation only, that is, the account is not an all-encompassing account of explanation, as some have mistakenly thought. Non-causal explanations, such as constitutive and mathematical explanations, are not dealt with here. Yet it is possible that constitutive explanations are similar to causal explanations, although the two differ insofar as their determination relation is concerned.[8] For instance, Carl F. Craver (2007: 139–160; see also his 2002) has

[8] By constitutive explanations I refer to explanations of property instantiations in which an explanation of a property of a system is given by its underlying nature. An example is an explanation of solubility of salt by reference to its molecular structure in which the latter explains and determines non-causally but asymmetrically the former. Anatomy and histology are biological disciplines that are looking for

made the suggestion that the explanatory relevance of constitutive explanations is based on their “mutual manipulability.” This, in turn, suggests that some forms of non-causal explanation do not significantly differ from causal explanation. Furthermore, even if the scope of this paper is limited, an important species of explanation is nevertheless discussed, for causal explanations allow controlling, changing, and manipulating nature in contrast to some non-causal forms of explanation.

Many philosophers and ecologists claim that ecological explanations (or results) amount to case studies or natural history, that is, to explanations that cannot be generalized to other taxa, places, times, and so on over and above those from which the explanations originally came (see Simberloff 1982; Sagoff 1985; Shrader-Frechette and McCoy 1993: 106–148, 1994). The reasons given are often the same or at least similar to the reasons given for why there are no ecological laws. A choice that traditional law-centered views have forced upon us is the distinction between (universal) laws and case studies. Curiously, the choice is made even by those who think that there is no (need for) biological laws (cf. Sharder-Frechette & McCoy ibid.). In a sense, I have presented the degrees between the two extremes. I have suggested that we have at our disposal ecological explanatory generalizations that are extrapolable. I argued that such invariant and stable generalizations function in the above-described manner despite the fact that they need not be lawlike as generalizations and despite the fact that these generalizations represent something more than “case studies.”

Acknowledgments This research was supported financially by the Emil Aaltonen Foundation. I am grateful to Markus Eronen, Petri Ylikoski, and referees for this journal that provided helpful comments on previous drafts of this paper.

References

Ashton KG, Tracy MC, Queiroz A (2000) Is Bergmann’s rule valid for mammals? Am Nat 156:390–415

Bechtel W, Abrahamsen A (2005) Explanation: a mechanist alternative. Stud Hist Philos Biol Biomed Sci 36:421–441

Bednekoff P (2003) Lawless biology. Am Biol Teach 65:167

Berryman AA (2003) On principles, laws and theory in population ecology. Oikos 103:695–701

Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann’s rule. Divers Distrib 5:165–174

Bogen J (2005) Regularities and causality; generalizations and causal explanations. Stud Hist Philos Biol Biomed Sci 36:397–420

Bonner JT (1968) Size change in development and evolution. In: Macurda DB (ed) Paleobiological aspects of growth and development. Paleontological Society, Michigan, pp 1–15

Brown JH (1995) Macroecology. University of Chicago Press, Chicago

Cartwright N (2002) Against modularity, the causal Markov condition, and any link between the two: comments on Hausman and Woodward. Brit J Philos Sci 53:411–453

Footnote 8 continued
constitutive explanations. Although in the case of constitutive explanations, there is a determination relation between “macro” and “micro” properties of a system, this determination relation is different from causal determination relation. Constitutive relations are synchronic and componentially related to their phenomena-to-be-explained, whereas causal relations are diachronic and non-componentially related to their phenomena-to-be-explained.

Cartwright N (2004) Causation: one word, many things. Philos Sci 71:805–819
Clutton-Brock TH, Harvey PH (1983) The functional significance of variation in body size among mammals. In: Eisenberg JF, Kleiman DG (eds) Advances in the study of mammalian behavior. American Society of Mammalogists, Shippensburg (Pennsylvania), pp 632–663
Colyvan M, Ginzburg LR (2003) Laws of nature and laws of ecology. Oikos 101:649–653
Connor EF, McCoy ED (1979) The statistics and biology of the species-area relationship. Am Nat 113:791–833
Cook RE (1974) Origin of the highland avifauna of Southern Venezuela. System Zool 23:257–264
Craver CF (2002) Interlevel experiments and multilevel mechanisms in the neuroscience of memory. Philos Sci 69:S83–S97
Craver CF (2007) Explaining the brain. Oxford University Press, New York
Darden L (2002) Strategies for discovering mechanisms: schema instantiation, modular subassembly, forward/backward chaining. Philos Sci 69:S354–S365
Darden L (2005) Relations among fields: Mendelian, cytological and molecular mechanisms. Stud Hist Philos Biol Biomed Sci 36:349–371
Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Belknap Press, Cambridge, pp 342–444
Durán LR, Castilla JC (1989) Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. Mar Biol 103:555–562
Gaston KJ (1996) Species-range-size distributions: patterns, mechanisms and implications. Trends Ecol Evol 11:197–201
Gilbert FS (1980) The equilibrium theory of island biogeography: fact or fiction? J Biogeogr 7:209–235
Glennan S (1996) Mechanisms and the nature of causation. Erkenntnis 44:49–71
Glennan S (2005) Modeling mechanisms. Stud Hist Philos Biol Biomed Sci 36:443–464
Gould SJ (1966) Allometry and size in ontogeny and phylogeny. Biol Rev 41:587–640
Hairston NG (1989) Ecological experiments. Cambridge University Press, New York
Hausman DM, Woodward J (1999) Independence, invariance and the causal Markov condition. Brit J Philos Sci 50:521–583
Hausman DM, Woodward J (2004) Manipulation and the causal Markov condition. Philos Sci 71:846–856
Hempel CG (1965) Aspects of scientific explanation. Free Press, New York
Hempel CG, Oppenheim P (1948) Studies in the logic of explanation. Philos Sci 15:135–175
Hitchcock CR (1995) Salmon on explanatory relevance. Philos Sci 62:304–320
Hitchcock CR, Woodward J (2003) Explanatory generalizations, part II: plumbing explantory depth. Noûs 37:181–199
Kitcher P (1989) Explanatory unification and the causal structure of the world. In: Kitcher P, Salmon WC (eds) Scientific explanation. Minnesota studies in the philosophy of science, vol 13. University of Minnesota Press, Minneapolis, pp 410–505
Lange M (2005) Ecological laws: what would they be and why would they matter? Oikos 110:394–403
Lawton JH (1996) Patterns in ecology. Oikos 75:145–147
Lawton JH (1999) Are there general laws in ecology? Oikos 84:177–192
Lewis D (1973) Counterfactuals. Basil Blackwell, Oxford
Loehle G (1990) Philosophical tools: reply to Shrader-Frechette and McCoy. Oikos 58:115–119
Machamer P, Darden L, Craver CF (2000) Thinking about mechanisms. Philos Sci 67:1–25
Mancosu P (2008) Explanation in mathematics. Stanford encyclopedia of philosophy. http://www.plato.stanford.edu/entries/mathematics-explanation/
Marquet PA (2000) Invariants, scaling laws, and ecological complexity. Science 289:1487–1488
Marquet PA, Quiñones RA, Abades S, Labra F, Tognelli M, Arim M, Rivadeneira M (2005) Scaling and power-laws in ecological systems. J Exp Biol 208:1749–1769
McKinney ML (1990) Trends in body-size evolution. In: McNamara KJ (ed) Evolutionary trends. University of Arizona Press, Tucson, pp 75–118
Mitchell SD (1997) Pragmatic laws. Philos Sci 64:S468–S479
Mitchell SD (2000) Dimensions of scientific law. Philos Sci 67:242–265
Mitchell SD (2002) Ceteris paribus—an inadequate representation for biological contingency. Erkenntnis 57:329–350
Mitchell SD (2008) Exporting causal knowledge in evolutionary and developmental biology. Philos Sci 75:697–706
Murray BG (1999) Is theoretical ecology a science? A reply to Turchin (1999). Oikos 87:594–600

Murray BG (2000) Universal laws and predictive theory in ecology and evolution. Oikos 89:403–408
Murray BG (2001) Are ecological and evolutionary theories scientific? Biol Rev 76:255–289
Murray BG (2004) Laws, hypotheses, guesses. Am Biol Teach 66:598–599
Nagel E (1961) The structure of science. Harcourt, Brace and World, New York
Newell ND (1949) Phyletic size increase, an important trend illustrated by fossil invertebrates. Evolution 3:103–124
O'Hara RB (2005) The anarchist's guide to ecological theory. Or, we don't need no stinkin' laws. Oikos 110:390–393
Owen-Smith N (2005) Incorporating fundamental laws of biology and physics into population ecology: the metaphysiological approach. Oikos 111:611–615
Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75
Paine RT, Vadas RL (1969) The effects of grazing by sea urchins, Strongylocentrotus Spp., on benthic algal populations. Limn Oceanogr 14:710–719
Pâslaru V (2009) Ecological explanation between manipulation and mechanism description. Philos Sci 76:821–837
Perini L (2005) Explanation in two dimensions: diagrams and biological explanation. Biol Philos 20:257–269
Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge
Peters RH (1991) A critique of ecology. Cambridge University Press, Cambridge
Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. Am Nat 100:33–46
Preston FW (1962) The canonical distribution of commonness and rarity: part II. Ecology 43:410–432
Psillos S (2002) Causation and explanation. Acumen, Chesham
Raerinne JP (2010) Allometries and scaling laws interpreted as laws: a reply to elgin. Biol Philos. doi: 10.1007/s10539-010-9203-9
Raerinne JP (2010) Generalizations and Models in Ecology. Dissertation, University of Helsinki, Finland
Rensch B (1960) The laws of evolution. In: Tax S (ed) Evolution after darwin, vol 1. University of Chicago, Chicago, pp 95–116
Sagoff M (1985) Fact and value in ecological science. Environ Eth 7:99–116
Salmon WC (1984) Scientific explanation and the causal structure of the world. Princeton University Press, Princeton
Salmon WC (1989) Four decades of scientific explanation. University of Minnesota Press, Minneapolis
Salmon WC (1994) Causality without counterfactuals. Philos Sci 61:297–312
Sandborg D (1998) Mathematical explanation and the theory of why-questions. Brit J Philos Sci 49:603–624
Shrader-Frechette K, McCoy ED (eds) (1993) Method in ecology: strategies for conservation. Cambridge University Press, Cambridge
Shrader-Frechette K, McCoy ED (1994) Applied ecology and the logic of case studies. Philos Sci 61:228–249
Simberloff DS (1974) Equilibrium theory of island biogeography and ecology. Ann Rev Ecol System 5:161–182
Simberloff DS (1976) Experimental zoogeography of islands: effects of island size. Ecology 57:629–648
Simberloff DS (1982) The status of competition theory in ecology. Annal Zool Fenn 19:241–253
Slobodkin LB (1964) Experimental populations of Hydrida. J Anim Ecol 33(Supplement):131–148
Steel DP (2006) Comment on Hausman and Woodward on the causal Markov condition. Brit J Philos Sci 57:219–231
Steel DP (2008) Across the boundaries. Oxford University Press, New York
Tabery JG (2004) Synthesizing activities and interactions in the concept of a mechanism. Philos Sci 71:1–15
Turchin P (2001) Does population ecology have general laws? Oikos 94:17–26
Williamson M (1989) The Macarthur and Wilson theory today: true but trivial. J Biogeogr 16:3–4
Wimsatt WC (1976) Reductive explanation: a functional account. In: Cohen RS, Hooker CA, Michalos AC, Van Evra JW (eds) PSA 1974. Reidel, Dordrecht, pp 671–710
Woodward J (2000) Explanation and invariance in the special sciences. Brit J Philos Sci 51:197–254
Woodward J (2001) Law and explanation in biology: invariance is the kind of stability that matters. Philos Sci 68:1–20
Woodward J (2002) What is a mechanism? A counterfactual account. Philos Sci 69:S366–S377
Woodward J (2003a) Making things happen. Oxford University Press, Oxford

Woodward J (2003b) Experimentation, causal inference, and instrumental realism. In: Radder H (ed) The philosophy of scientific experimentation. University of Pittsburgh Press, Pittsburgh, pp 87–118
Woodward J (2006) Sensitive and insensitive causation. Philos Rev 115:1–50
Woodward J (2010) Causation in biology: stability, sensitivity, specificity, and the choice of levels of explanation. Biol Philos 25:287–318
Woodward J, Hitchcock CR (2003) Explanatory generalizations, part I: a counterfactual account. Noûs 37:1–27
Ylikoski P, Kuorikoski J (2010) Dissecting explanatory power. Philos Stud 148:201–219