Analogical Thinking in Ecology: Looking Beyond Disciplinary Boundaries

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Abstract: We consider several ways in which a good understanding of modern techniques and principles in physics can elucidate ecology. We focus on analogical reasoning between these two branches of science. This style of reasoning requires an understanding of both sciences and an appreciation of the similarities and points of contact between the two. In the current ecological literature on the relationship between ecology and physics, there has been some misunderstanding about the nature of modern physics and its methods. Physics is seen as being much cleaner and tidier than ecology. When ecology is compared to this idealised, fictional version of physics, ecology looks very different, and the prospect of ecology and physics learning from one another is questionable. We argue that physics, once properly appreciated, is more like ecology than ecologists have thus far appreciated. Physicists and ecologists can and do learn from each other, and in this paper we outline how analogical reasoning can facilitate such exchanges.

1. Introduction

Ecology and physics have different subject matters and, on the face of it at least, quite different methods. But still there are similarities. For example, they both employ similar mathematical methods. There has been a lively, on-going discussion about the similarities and differences between ecology and physics (e.g. Berryman 2003, Lange 2005, Lawton 1999, O'Hara 2005, Quenette and Gerard 1993, Turchin 2001). This discussion has revolved around two main themes: whether ecology has laws like those of physics, and whether it is fruitful to employ some of the methods of physics in ecology. Although these issues are both of considerable interest and are closely related, we will focus mainly on the second, more general issue. We argue for a specific sense in which ecology can be advanced by looking towards physics. We argue that analogical reasoning between different branches of science is a very fruitful means of generating new hypotheses. In particular, we argue that advances have been made, and will continue to be made, in ecology as a result of keeping watchful eyes on ideas from physics and emulating some of the more successful strategies. Sometimes this involves exploring the idea that ecology has laws not unlike the laws of physics, sometimes it involves thinking about the appropriate number of dimensions to formulate ecological theories as is common in physics.

First, we discuss some of the reasons advanced in support of the view that physics and ecology are different. After all, if ecology and physics are radically different, then it may be fruitless for ecologists to try to learn from physics. We will argue that ecology and physics are not so different. The alleged dissimilarities between the two are (unintentionally) exaggerated by some participants in the debate and this exaggeration would seem to be a result of holding an idealised, unrealistic picture of how physics operates. With the misconceptions about physics cleared away, the differences between ecology and physics are much less significant.

We then discuss three examples of where ecology has made advances or where advances might occur as a direct result of analogical reasoning of the kind we advocate. We finish by showing that this is not "physics envy" on our part; we believe that the use of analogical reasoning across different branches in science is generally very useful and is already widely used in physics. We also give a couple of examples where physics has learned from ecology and evolution via analogical reasoning. Throughout the discussion we argue for similarities between ecology and physics but we do this in order to show why these similarities matter: both ecology and physics are advanced by appreciating the similarities and availing themselves of analogical reasoning to make the relevant connections.

2. Ecology and Physics are Not So Different

We use Dale Lockwood's (2008) recent paper as a clear and carefully-articulated example of the case for the dissimilarity of physics and ecology. We should make it clear that Lockwood is not addressing the specific issue of analogical reasoning that we are interested in. Rather, his primary focus is on arguing against the claim that there are laws in ecology, but in attempting to do this he touches on several important points about the alleged differences between physics and ecology. We suspect that he speaks for many on these issues. In any case, his paper presents a forceful case that needs addressing and provides a useful point of departure for the discussion of this section.

Lockwood starts by suggesting that he will set aside the issue of whether there are laws in physics and focus on whether there are laws in ecology. But as his own discussion demonstrates, and as we argued previously (Colyvan and Ginzburg 2003b) this is hard to do. The problem is that the best examples of laws are in physics, so one can either use those laws to serve as the basis for a definition of "law" and see whether the alleged laws of ecology measure up to that definition, or, alternatively, you can directly compare the alleged laws of physics with their counterparts in ecology. Given the extreme difficulty in providing an adequate definition of "law", we (Colyvan and Ginzburg 2003b, Ginzburg and Colyvan 2004) opted for the latter strategy, concluding that either ecology does have some good candidates for laws or there are no laws in physics either (Colyvan and Ginzburg 2003b). Lockwood (2007, 2008) is a little bolder than we were and opts for the former strategy of offering a definition (or at least a working definition) of a law as "a factual truth that is spatiotemporally universal, supports counterfactuals, and has a high level of necessity." (Lockwood 2008, p. 58)

As definitions of “law” go, Lockwood’s is not a bad one, but it would seem to rule out the existence of laws in physics. Although Lockwood says that he wishes to leave the issue of laws in physics aside, he adopts a definition of “law” so stringent that it rules out most of the usual candidates for laws anywhere. He is thus left advancing a general eliminitivist position about laws, according to which there are none. This was one of the options we left open, but we find it a rather unattractive option. Rather than set the bar so high for lawhood that there are none, it is better to be less stringent about what counts as a law—hence our countenance of laws with exceptions, laws with *ceteris paribis* clauses, and the like. Indeed, given that Lockwood goes on to argue for the differences between physics and ecology, we take it that he does not in fact mean to be advancing such a general elimination of laws. He does, it seems, believe that there are laws in physics and that his definition is adequate to capture them. We believe he is mistaken about the adequacy of his definition of “law”, but the reasons for his mistake are both interesting and informative.

Lockwood takes laws of physics to be temporally universal: they are supposed to hold for all time. But in physics it is routinely suggested that the current laws of physics did not hold during the very early period of the universe. We take part responsibility for this mistake, for we (and others) have focussed on very simple cases from physics, namely, Newton’s laws. We did this for reason of ease of exposition. Perhaps there was a time when Newton’s laws were thought to be universal in this sense, but modern laws in physics (if there are any) are generally no longer thought of in this way. Lockwood’s mistake is to generalise from a limited number of simple cases from physics. In effect he takes physics to be cleaner and simpler than it really is. Ecologists, more than anybody, are aware of the complexities and difficulties in ecology. It is not surprising that when you consider a realistic and accurate picture of ecology (as Lockwood so admirably paints) and you compare this with an idealised, high-school-level cartoon of physics, ecology comes out looking messier. As it turns out, almost all the claims that Lockwood makes about the failings of the candidate laws in ecology straightforwardly carry over to physics (once physics is properly understood). Lockwood points out the lack of additivity in ecology without realising that this is also the case in physics (e.g. velocities in special relativity do not simply add). Lockwood points out that in ecology there is a choice about how to represent the dynamics, but again this is the same in physics. There are different ways to represent quantum mechanics (e.g. Dirac’s and Hilbert’s), as well as several different interpretations of the formalism (Hughes 1989). Even in classical Newtonian mechanics there are Laplacian and Hamiltonian formulations (see Lyon and Colyvan 2008 for the significance of these different formulations). Lockwood notes that there is underdetermination of theory by data in ecology, but fails to appreciate that this is so in physics as well (see Duhem 1954, Lakatos 1970, and Quine 1980 on this). There are also a number of contentious points in Lockwood’s paper, such as non-standard views about logic and logical possibility and what the counterfactual dependency requirement for laws involves. These points, however, do not bear directly on our purposes here, so we set them aside. There are, however, two claims that Lockwood makes that deserves closer inspection.

Lockwood suggests that laws in physics are exceptionless and discusses our example of a snowflake and a rock falling with different accelerations, contrary to Galileo's law that acceleration is independent of mass. Lockwood is quite right to point out that Galileo's law can be saved by positing differential friction from air resistance in the two cases. Moreover, he is correct that this is the standard account of how to understand such apparent violations of the law in question. Lockwood fails, however, to realise that such a move can *always* be made, and indeed can be made in ecology as well. Whenever we see a population not growing according to the logistic equation, say, there is nothing to stop us from positing some complicating factor that saves the logistic equation. While it might be tempting to suggest that the difference between these two cases is to be found in the empirical testability of the posited complicating factors, this will not do. The empirical demonstration of the complicating factors involved in the apparent failure of the logistic equation is straight forward—it is seen in the failure of the population to grow according to the logistic equation. This might seem *ad hoc* and even circular, but it is no more circular or *ad hoc* than similar cases in physics (e.g. conservation laws). It is very common to count as an empirical demonstration of some effect, a deviation from a relevant law.

On a related point, Lockwood claims a difference between physics and ecology in that idealisations required to get the laws to work in ecology are "unrealistic". But the idealisations in ecology are no more unrealistic than the idealisations in physics: point masses, inertial reference frames, incompressible fluids and the like? As we suggested in our earlier paper, the appropriate way to understand laws like Newton's first law (all bodies move with uniform motion unless acted upon by a force) is not in terms of describing any actual system. Maybe Lockwood is right and there are some systems with zero net force acting on them (although it is not clear that his examples of books sitting on shelf on a planet rotating on its axis and orbiting a star which is in turn rotating around the galactic centre are the best examples for his purposes). In any case, the laws of physics are not merely about such special cases (if there are any). Newton's first law is supposed to inform us about other systems as well. Laws provide background conditions from which departures need to be explained (Ginzburg and Colyvan 2004). Think of Newton's first law as a complicated counterfactual about what would happen if a system were isolated from all forces, or as a description of an idealised system that has some similarity to the system under consideration. Once the role of such laws in physics are appreciated, we see that Lockwood's remarks about the candidate laws in ecology being about ideal populations and thus unrealistic is exactly right, but, contra what he goes on to conclude, this is precisely why these *are* good candidates for laws. According to the view of laws we advocate, invoking unrealistic ideal set-ups is precisely what we should expect from a law. Most importantly, for present purposes, physics and ecology are alike in this regard.

3. Analogical Insights from Physics

For all that has been said so far, there is no reason to take physics and ecology to be so different that one cannot learn from the other. In particular, we have argued that there is no good case for physics being law governed while ecology is not. With this much of a connection in place, we want to proceed to establish the usefulness of borrowing methods and insights across these two disciplines. The question of how often such borrowing has occurred is an interesting historical question. Although there is evidence for at least some such borrowing, we do not need to establish historical precedence in order to make our case. Our claim is about the usefulness of such borrowing. In order to demonstrate this, we do not need to establish that there has been borrowing on a regular basis and that it has mostly been useful. Although that would suffice for our case, if true, that would likely be old news. Alternatively we could argue directly for the usefulness of the kind of analogical reasoning we have in mind. This can be done by showing that the kinds of analogies in question could plausibly lead to advances in the relevant theories. We will employ both strategies, giving some historical evidence that the analogical thinking we have in mind has been used to good effect, but also offer other cases where it is at east plausible that analogical reasoning has been or might have been employed to good effect.

We now turn to the details and specific examples of how ecology can learn from physics. We show how adopting some of the mathematical techniques employed in physics, by way of analogy, can be useful in ecology.

3.1 Time as the fourth dimension in metabolic ecology

One example demonstrating the potential of analogical thinking in ecology is the consideration of the dimension of the biological organism. The issue arises out of metabolic ecology, the field where metabolic rates are studied as a function of body size. It is not just metabolic rates but rates of reproduction, longevity of organisms, and even their geographic density that happen to relate to body size in interesting ways. The best recent reference to the subject is a review by Brown *et al*. (2004) and a popular book by Whitefield (2006). A long-standing problem in this area is to explain why metabolic rate scales as 3/4 power of body size rather than 2/3. Originally it was suggested (Rubner, 1883) that metabolism as a property of surfaces is quadratic with a linear dimension while body size (weight) is cubic, so 2/3 was the expected slope of the line, when metabolism is plotted against body weight (in log scales). Klieber (1932) had discovered, however, that in the interspecies comparison, 3/4 is a better approximation.

The suggestion that a fourth dimension of some sort is involved in explaining the 3/4 power is over 30 years old (Blum, 1977). That time may play that role was also briefly suggested by Hainsworth (1981) in his well-known book on physiology. The picture clarified recently with the suggestion (Ginzburg and Damuth, 2008) that generation time may well be the missing fourth dimension, to be added to the three spatial dimensions. On this view, 3/4 is the expected power in cross-species comparisons where there are great differences in generation times. The power in question is predicted to be 2/3 within a single species, where sizes differ but longevity does not. The power can even be 1/2 if, in addition to placing constraints on the time dimension (e.g. by fixing generation time), one also constrains one of the spatial dimensions (e.g. by comparing only humans of a particular height).

We will not bother with the details here—they are not important for present purposes. Our point is simply that the insight from physics of seeing time as a fourth dimension and thinking of objects as four-, rather than three-dimensional, can, and has, served as a springboard to consider generation time as a natural and inseparable dimension of an organism. The idea of linking space and time and thinking of them as different aspects of the one thing (the space-time manifold) was developed to great advantage in physics over 100 years ago. The move to space-time as the basic framework in physics served as inspiration for investigating the analogous idea in ecology (Ginzburg and Damuth, 2008). The idea is that in physics some phenomenon (e.g. the Lorentz contraction) is puzzling when considered in a three dimensional framework, but is exactly what one would expect when the phenomenon in question is considered in a four-dimensional space-time framework. The central idea of Ginzburg and Damuth (2008) was to explore the idea as a way of approaching the puzzling 3/4 power appearing in metabolic ecology.

But even without the historical case, it should be clear that thinking about organisms in this four-dimensional way, might have been arrived at via analogical reasoning from Einstein's relativity theory. Recall, that we are arguing that such thinking can be employed and can prove to be fruitful; we are not arguing that it is already a regular part of ecological methodology. It should also be clear that this four-dimensional approach to the allometries of metabolic ecology appears to be a fruitful line of research, although, admittedly, only time will tell whether it is ultimately correct. We thus have a case of analogical reasoning from physics, allowing the formulation of new hypotheses in ecology, even though there are significant differences between the origin of the idea in physics and the application to scaling relationships in metabolic ecology. We also note that there is no suggestion of common cause here. (Indeed, it is not even clear that the relevant physics is in the business of providing causal explanations (Colyvan 2001, pp. 50–51).) Rather, the analogy allows one to see abstract structural similarities and this insight opens up interesting lines of ecological research. On our view, there do not need to be common causes or even similar causal networks in place in each case, abstract structural similarity alone is enough to generate the hypotheses in question. Testing of the hypothesis is then conducted in the usual ways and will no doubt, prompt further work on understanding causal mechanisms, where appropriate.

3.2 Ratio-dependent predation versus law of mass action

Models of species interaction have relied on analogies from physics ever since their original appearance nearly 100 years ago. Lotka's 1924 book was entitled "Elements of Physical Biology". It was reprinted in 1956 as "Elements of Mathematical Biology" (Lotka, 1956) an erroneous editorial change, in our opinion. The original title explicitly emphasises the connections between ecology and physics. Volterra (1931), independently of Lotka, used the image of random encounters which was basic for physical chemistry, a subject in which Lotka majored in college. A more recent suggestion which complements the classical Lotka-Volterra model is based on a simple invariance or symmetry.

The notions of invariance and symmetry are central to a great deal of modern physics. Richard Feynman (1965) gives a typically clear account of invariancy of physical law with respect to translation in space, whereby only relative distances matter. This symmetry, however, is not perfect but is a very useful approximation that holds almost everywhere.

Analogous to spatial translation (adding the same value to all spatial coordinates of a given physical system), there is a symmetry in the interaction of a consumer population with the resource it consumes. Interaction will be approximately constant if we multiply both the resource abundance and the consumer abundance by the same factor. Just as with physical invariancy, it does not hold perfectly and universally. For example, when consumers are rare their growth will depend on the resource density itself, and not on the per capita density (since their home ranges will not overlap). For a substantial range of values, however, the invariancy holds. This has been noticed long ago by Contois (1959) when he grew *E.coli* in chemostat. He determined that the growth rate is a function of per capita sugar, rather than absolute sugar concentration.

The invariancy under discussion has become known as *ratio-dependent predation* (Arditi and Ginzburg, 1989) and has attracted considerable attention in ecology (reviews by Abrams and Ginzburg, 2000, Jensen and Ginzburg, 2005), eventually entering the latest editions of standard ecology textbooks (Begon *et al*, 2006, Krebs 2008). Without going into the details of when this invariancy is or is not a good approximation, we just draw attention to the analogy with translation invariance in physics. In fact, when viewed in logarithmic scale, as is the custom in ecology, the two principles are mathematically identical. We stress, however, that in both cases the invariances are only approximate and are violated in extreme situations.

Invariance is a central concept and, in particular, for an adequate understanding of some phenomenon we need to know when the phenomenon in question is changed and when it is not (i.e. what it is invariant with respect to). This we learned from physics long ago and it turns out also to be useful in ecology, albeit the idea is put to different use in the ecological setting. Such analogical thinking opens up new possibilities, which in some cases could not even be entertained. For example, exponential growth of both predator and prey is a possibility in the ratio-dependent view, but not on the standard Lotka-Volterra model. (It is interesting to note that in economics there are "balanced growth" models and these allow joint coordinated exponential expansion across several sectors (Cooley 1995).) The core of the ratio-dependent predation debate is whether Malthusian growth is truly fundamental in ecology or whether it disappears as species interact.

Even though the Lotka-Volterra model is not invariant, when the consumer density is low, the physical image the model suggests works better, since interference in consumption can be ignored. At the other extreme, when the density is high, interference is nearly perfect and ratio dependent analogy works (Abrams and Ginzburg, 2000). Both models turned out to use physical analogies, just different ones. Both have their domains of applicability. The existing tension is not about which one is right but rather concerns the clear delineation of the domains of validity.

3.3 Inertia in population growth

The suggestion that exponential growth (Malthus' law) in ecology is analogous to Newton's first law in physics is over 20 years old (Ginzburg, 1986) and has since been adopted by others in ecology (e.g. Turchin, 2001). Taking exponential growth to be the default state focuses attention on departures from unrestricted exponential growth and on the rate of change of population growth (rather than rates of population growth). In more mathematical terms, this is to say that the population growth of a single species may be viewed as a two-dimensional process with another variable, in addition to abundance in joint simultaneous dynamics. It is important to note that the analogy with physics here is clear and is quite explicit in all the key publications on the topic (e.g. Ginzburg 1986; Colyvan and Ginzburg 2003a). Thinking about inertia in physics led to the inertial view of population dynamics via analogical reasoning, and it is a very natural chain of reasoning when viewed from a suitably abstract point of view (Ginzburg and Colyvan 2004).

One likely candidate for such a "hidden" variable is individual quality and the mechanism of interaction is the so-called maternal effect. That the maternal effect can result in second-order dynamics of single species is an idea that is at least 50 years old (Wellington 1957). In its quantitative form it has been developed in the 1990s and is summarized in Colyvan and Ginzburg (2003a), Ginzburg and Colyvan (2004) and also sympathetically discussed in Wagner (2005). The maternal effect as a mechanism for population cycles due to second-order internal dynamics remains a lively research area, with a large number of publications, including good experimental work (see review by Inchausti and Ginzburg, 2009). Just as in the case of ratio dependence above, the inertial idea of population dynamics is also finding its way into ecology textbooks, (Begon *et al*, 2006) albeit as a minority and somewhat controversial view, but one worthy of investigation. The dominant view of the source of deviations from exponential growth is species interactions such as predator–prey relationships. It is our opinion that the relative emphasis on internal (inertial) versus external reasons for population dynamics may shift in the future towards a more pluralist approach, where several mechanisms for departures from exponential growth are recognised. In any case, the analogy between exponential growth in ecology and uniform motion in physics has delivered an interesting new approach to population dynamics. The ultimate fate of this new approach is yet to be determined but if it finds acceptance, the analogical reasoning in question will have led to genuine progress.

There are other examples of analogical thinking, both actual (such as the explicit use of analogies from the physics of chemical reactions by Lotka to model population interactions (Kingsland 1985)), and potential (other examples of where thinking in terms of symmetries might prove fruitful). But we trust we have made our point that analogical thinking from physics can and has been used to good effect in ecological theory building.

4. Analogical Insights from Evolution

In this section we show that the kind of analogical reasoning we are advocating is a two-way street. We are not simply advocating a kind of physics envy, where ecologists should try to emulate the feats and methods of physics. We believe that physics can and has learned a great deal from biology, via this same kind of reasoning. An obvious and well-known example here is the groundbreaking work of Robert May (1973) on stability and bifurcations in population equations. This work was important in the development of chaos theory and opened the way for a better appreciation of complex systems, wherever they occur—ecology, physics or elsewhere. Here we focus on a couple of less well-known examples, examples where it appears that physicists have learned from one of the giants of biology: Charles Darwin.

4.1 Anthropic reasoning

There is an interesting question in cosmology concerning the so-called "fine tuning" of the universe. It turns out that many of the physical constants, such as the electron–proton mass ratio and the fine structure constant could not have been more than a few percent different from their actual value without resulting in a radically different universe. In particular, were some of these constants to be just slightly different, the universe would not contain carbon-based life and consciousness (Barrow and Tipler 1986, Cf. Weinberg, 1993). It appears that the universe is tailor made for life. A variety of hypotheses have been advanced to account from this surprising fine tuning of the universe, from religious intelligent-design hypotheses to multiverse hypotheses. Let us consider the more serious scientific response: the multiverse hypothesis.

According to the multiverse response there are many universes, either via many big bangs or island universes arising from a single big bang. The details need not concern us. The main idea is that these universes are created with variation—perhaps random variation—of the many physical constants appearing in the laws of physics. We thus end up with infinitely many universes and in keeping with the fine-tuning observation, very few of them contain carbon-based life or consciousness. Under this hypothesis, there is no puzzle as to why there is *some* universe with the physical constants required for carbon based life, just as there is no puzzle about why after infinitely many card shuffles there was one shuffle that left the cards arranged in descending suit order. The only puzzle left is why does *our* universe contain life. The anthropic principle is now invoked. This principle is a selection principle and states that only universes with consciousness in them will have agents capable of wondering about their own and other universes. So again there is no puzzle about why we find ourselves in one of the universes with consciousness: for we are conscious and universes without consciousness do not have anyone to be puzzled. It is also not too much of a stretch to argue that universes with consciousness have to contain life of some sort (if not carbon-based life).

We are not endorsing or defending this line of response here (see Colyvan *et al.* 2005 for another line of response), but this is a serious scientific hypothesis, endorsed by quite a few physicists. Importantly, for present purposes, this response owes a great deal to Darwin. The fine-tuning argument, after all, is simply a reworked design argument, structurally the same as Paley's biology-based design argument. Instead of Paley's appeal to the adaptation of organisms to their environments and praising the virtues of various human organs (such as the eye) for survival purposes, the new design argument appeals to the fine tuning and the presence of life itself in the universe. And the multiverse response combined with the anthropic principle is analogous to genetic variation and natural selection as a response to the original design argument. Focussing on the similarities between these two design arguments leads to an interesting Darwin-inspired response to the fine-tuning argument. A related response to fine tuning is the fecund universe theory (Smolin 1997) according to which universes produce daughter universes and natural selection operates to favour those universes likely to have plentiful offspring. In the standard multiverse theory, the analogy with Darwinian evolutionary theory is clear enough, but in fecund universe theory, the analogy carries over in almost every detail. Moreover, in fecund universe theory, the Darwinian inspiration is quite explicit.

4.2 Gravitational exclusion

While the anthropic principle example just discussed is a direct application of Darwinian evolution model (there is both "mutation" when universes reproduce and "selection" via the anthropic principle), our next example—the evolution of the solar system—is a little different. Planets or the initial particles that formed them do not reproduce but they are certainly subject to a kind of "exclusion". Some of these particles joined the "planetesimals", and protoplanets, while others fell into the Sun. In all cases, we view what we see today as a result of an historical process of elimination. This is a view present in all the theories of the 20th century, including the now discredited Chamberlin-Moutton theory: a biparental theory where planets grew from the encounters between the Sun and another star (Brush 1996). The prevailing current view is uniparental: all the initial material came from the one source, a supernova, which provided the material for the Sun, the planets, and the asteroids. This initial material is assumed to have been widely and randomly distributed (providing the celestial analogue of the biological random mutation). This material was then subjected to a kind of stability selection, whereby the particles in unstable regions of space would be draw from those regions, thus increasing the number of particles in stable regions. We thus have a celestial analogue of differential selection. Recent discoveries of planets around many distant stars, behaving very much like our own, is the single strongest argument towards the current view, even though there are other, more-direct arguments (Brush 1996). The current gradual and evolutionary-like theories are very different from the 19th century views of the meteoric origin of planets. On this 19th century view, planets were originally meteors caught by the Sun's gravitational field. The impact of Charles Darwin here is clear. He created an intellectual climate of evolutionary and selectionist thinking in biology and this, it would seem, was appropriated, to good effect, by astronomy.

A further example of this *gravitational exclusion* can be seen directly in the asteroid belt and the rings of Saturn. The rings of Saturn are relatively stable but there are elliptical gaps representing unstable orbits. Any particle drifting into these regions will be dragged out again by the gravitational forces exerted by nearby bodies. Similarly, there are well-known gaps in the asteroid belt between Mars and Jupiter: the Kirkwood gaps. These gaps represent unstable orbits, selected against by the dynamics of the gravitational system of which they are a part (Arnol'd 1990). Again, this gravitational exclusion is similar to the competitive exclusion in ecology. (It might seem that this analogy is a little stretched. After all, as we have already pointed out, the gravitational exclusion case has no obvious analogue of reproduction. It has *selection*, and that selection is *natural* (it is due to gravitation), but there is no *natural selection*. Be that as it may, it is also clear that even partial analogies like this can be fruitful.)

An interesting consequence of gravitational exclusion is that the unstable regions often place the surviving bodies at some distance from one another and this allows these bodies to be treated via the relatively simple Kepler laws (essentially treating the interactions of primary interest as two-body problems, enabling us to ignore other gravitational influences). We speculate that ecological allometries, the ecological analogue of Kepler's laws (Ginzburg and Colyvan, 2004) may be explained by ecological elimination, similar to the simplicity arising from Kepler's laws evolving by gravitational exclusion.

The message to be gleaned from this section is that it would appear that physicists took natural selection seriously and it affected the way they thought about a variety of phenomena in the 150 years since Darwin published the theory of natural selection. Even if they didn't explicitly appeal to biological analogies, the intellectual climate after Darwin facilitated the making of such connections, and the connections are plain to see. The result has been several evolution-inspired advances in physics.

5. Conclusion

We have argued that we should not limit ourselves in where we look for new ideas, and, in particular, analogies drawn from other scientific disciplines are a legitimate and potentially fruitful means of generating new ideas. Drawing attention to differences in kind between branches of science is counterproductive: electro-magnetism learned from gravitation, evolution and economics have learned from each other. Instead, we should notice the points of contact and similarities between disciplines. No doubt, there are differences as well, but we should not let the differences blind us to the similarities and the lessons we can learn from other branches of science. Indeed, as science progresses with more and more specialised sub-disciplines emerging, each with their own stock of tools and methods, the importance of one group of researchers learning from others via analogical thinking may become even more important.

The examples we presented are cases where analogical reasoning between ecology and physics has (at least potentially) enriched each discipline. Often this analogical reasoning is conducted by invoking the resources of mathematics, where abstraction away from detail helps in the appreciation of structural similarities (Colyvan 2001; 2002). At the very least, analogical thinking can give practitioners another means by which interesting hypotheses, candidate laws, and theories can be generated. Of course the hypotheses, candidate laws, and theories in question need to be tested by the standards of the discipline in question. The suggestions in section 3 need to be scrutinised and subjected to ecological confirmation or disconfirmation; the examples of section 4 need to be subjected to the scrutiny of physicists.

There are undoubtedly dangers associated with analogical reasoning. Physics and ecology are different and they use different methods. Analogies between the two can be stretched too far and when this occurs analogical thinking may well impede scientific progress. Ill-advised analogies might invite the acceptance of assumptions warranted in one domain but not in another, and might even lead to faulty experimental designs (Mikkelson 1997). But our claim is not that analogical thinking will always prove to be fruitful, just that sometimes it can be. And our claim is not that there are no dead ends and pitfalls associated with analogical thinking; we simply claim that just such thinking does not always lead to trouble. Indeed, the scientific enterprise itself offers no guarantees that any particular instance of a method will not mislead or lead to dead ends, so analogical thinking is no different from other tools in the scientific toolkit in this regard.

Newton once remarked that he had been fortunate enough to stand on the shoulders of giants. The giants he was referring to were probably Aristotle, Descartes, Galileo, Kepler, and others—all giants of physics (as well as giants of mathematics and philosophy in some cases). Ecologists and biologists have no hesitation in learning from the giants of their own respective disciplines, Lotka, Volterra, MacArthur and of course Darwin. We have no quarrel with this; our suggestion is a modest one. We simply suggest that there is no need to limit ourselves to the giants of ecology and biology—any giant will do: Newton, Darwin, Einstein or Volterra. There are, no doubt, wondrous things to be seen from any of these shoulders.

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