Integrative Pluralism *

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Abstract. The 'fact' of pluralism in science is no surprise. Yet, if science is representing and explaining the structure of the *one* world, why is there such a diversity of representations and explanations in some domains? In this paper I consider several philosophical accounts of scientific pluralism that explain the persistence of both competitive and compatible alternatives. Paul Sherman's 'Levels of Analysis' account suggests that in biology competition between explanations can be partitioned by the type of question being investigated. I argue that this account does not locate competition and compatibility correctly. I then defend an integrative model for understanding pluralism. This view is based on taking seriously both the complexity and contingency of biological organization and the idealized character of biological models. On this view, explanation becomes, among other things, the location for the integration of diverse models. I explicate my argument by an analysis of explanations of division of labor in social insects.

Key words: complexity, division of labor, idealization, levels of analysis, pluralism, self-organization

The 'fact' of pluralism in science is no surprise. On scanning contemporary journals, books, and conference topics in some sciences, one is struck by the multiplicity of models, theoretical approaches, and explanations. Yet, if science is representing and explaining the structure of the *one* world, why is there such a diversity of representations and explanations in some domains? One response is that pluralism simply reflects the immaturity of the science (Kuhn 1962). Yet history shows us that many sciences do not exhibit a diminution in the multiplicity of theories, models, and explanations they generate. This 'fact' of pluralism, on the face of it, seems to be correlated not with maturity of the discipline, but with the complexity of the subject matter. Thus the diversity of views found in contemporary science is not an embarrassment or sign of failure, but rather the product of scientists doing what they must do to produce effective science. Pluralism reflects complexity. In this

paper I will consider several philosophical accounts of scientific pluralism. I will then defend an integrative model for understanding compatible alternatives and illustrate my position by an analysis of explanations of division of labor in social insects.

Competitive vs. compatible alternatives

To understand scientific pluralism, we need the distinction between what I call competitive and compatible pluralism (Mitchell 1992; Mitchell et al. 1997). Almost all recent philosophers of science concerned with pluralism have concentrated exclusively on competing hypotheses, like the wave and particle theories of light or Darwinian and Lamarckian theories of inheritance (for exceptions see Cartwright 1994; Dupré 1993, 1996; Hacking 1996). Feyerabend (1981) and Lakatos (1978) writing in the Popperian tradition endorsed the desirability of maintaining a number of competing research programs or theories in order to hasten progress in science. The argument is that competition among alternative accounts of the same set of phenomena present the most severe environment for the testing of any one individual account. For these writers, scientific growth occurs by exposing false hypotheses or weak portions of a research program to empirical scrutiny and then rejecting the offending hypothesis or strengthening the weak assumption. In this framework, having a plurality of competing alternatives is supposed to increase the probability that particularly troublesome empirical results for any given hypothesis will be exposed.

Competitive pluralism also has been defended from a different perspective, by Beatty (1987) and Kitcher (1991). For them, maintaining multiple, competing theories and explanations is deemed the rational strategy to adopt for the scientific community as a whole in order to hedge its bets against empirical uncertainty. Given our epistemological fallibility, one cannot reliably project that the theory which accrues the highest epistemic warrant based on current empirical support will continue to win out in the light of future findings.

So, while these two approaches acknowledge and endorse the maintenance of competitive pluralism, the ultimate aim of science is to resolve the conflicts by adopting the single unfalsified, or 'true', or overwhelmingly supported winner of the competition. As Kitcher puts it, 'The community goal is to arrive at universal acceptance of the true theory' (Kitcher 1991: 19). The slogan here might be 'Pluralism: the Way to Unity.' These accounts of competitive pluralism presume that pluralism is temporary and strategic, but ultimately eliminable. While this analysis correctly describes some of the diversity of models and explanations found in contemporary science, it fails

to capture all of it. The remainder is constituted by compatible, not mutually exclusive, alternatives.

Biologists have long recognized the diversity of compatible explanations. Mayr (1961, 1982) distinguished between *how* and *why* questions that one may ask of nature. This distinction was introduced in an effort to protect the autonomy of separate biological traditions from a perceived threat of reduction and elimination (Beatty 1994). Later Tinbergen (1963) outlined a four-part classification of questions one might ask of a biological phenomenon. Recently Sherman (1988, see also Reeve and Sherman 1993) revived these approaches under the name 'levels of analysis'. Biological questions are separated into levels of evolutionary origin, current reproductive function, ontogeny, and mechanism. Questions at different levels require different answers (see Van Fraassen 1980).

Answers could only compete; the argument goes, if they were addressed to the same question or level of analysis. Sherman says, "Every hypothesis within biology is subsumed within this framework; competition between alternatives appropriately occurs within and not among levels" (Sherman 1988: 616). While there are valuable insights in this account of compatible pluralism, *the levels of analysis framework fails to adequately represent the relations between alternative explanations*. I will argue that it misconstrues where conflict does and should occur and where alternatives are correctly judged to be compatible. In the extreme case, it can lead to a form of isolationism that can impede answering questions within any single level. The mistake of the levels of analysis approach lies not in recognizing a diversity of questions – indeed scientists do pose a variety of questions to the subjects they study – but rather in the assumptions made about the epistemological structure of the answers. That is, scientific explanations often are causal explanations, identifying the set of conditions that give rise to the phenomenon of interest. At the same time, complex phenomenon harbor multiple interacting causal processes and multiple levels of organization which all may be involved in the generation of the feature to be explained. By disambiguating the question to be answered by an explanation – i.e. what is the evolutionary origin of a trait or behavior we observe now – one is still left with a plurality of potential causes acting at a number of levels of organization which may well constitute compatible answers to that single question.

The case of division of labor

In order to show that the levels of analysis model of compatible pluralism is mistaken, and defend the need for an alternative view, I will consider the example of explanations of division of labor in social insects. A social insect

colony is a complex system. Compositionally it is complex, being constituted by a whole made up of many, nonrandomly structured parts. Dynamically it is complex in that it is the location for multiple, interacting causes some of which are represented as linear functions, some as non-linear functions. And evolutionarily it is complex in that social insects display a variety of historically contingent, adaptive responses to environmental challenges.

Evolved variability is significant in understanding how multiple causal models may be brought to bear on the explanation of a particular system or event. Given the irreversible nature of the processes of evolution, the randomness with which mutations arise relative to those processes, and the modularity by which complex organization is built from simpler components, there exists in nature a multitude of ways to 'solve' the problems of survival and reproduction. Relative, not optimal, adaptive peaks characterize the direction in which evolutionary change occurs. This implies that diverse adaptations, even under the same or similar environmental conditions and even in closely related species and genera, are likely to arise in nature. As I will argue below, this has important implications for the generality of explanatory models in biology.

A social insect colony consists of tens of thousands of individuals engaged in a variety of behaviors including cell cleaning and capping, brood and queen tending, comb building, cleaning and food handling, and guarding and foraging (see Winston 1987). The individuals are not randomly engaged in tasks, nor does each individual do all the jobs required. This latter pattern describes solitary insect behavior, and it is from solitary insects that social insects evolved. Division of labor in the social insects refers to patterns of variation among workers within a colony in the tasks they perform (Oster and Wilson 1978). These patterns include 'age-polyethism', homeostatic regulation and individual specialization. Age-polyethism refers to the regular changes of tasks performed through the life of the typical individual worker. Young individuals work inside the hive, older individuals work outside. For bees, four age 'castes' have been distinguished: 1. cell cleaning, 2. brood and queen care, 3. food storage, and 4. foraging. Each 'caste' consists of a repertoire of tasks, and the individuals vary in their degree of specialization within a caste set.

In addition the colony as a whole displays plasticity by adjusting the proportions of workers active in particular tasks in correspondence to both internal and external factors. If there is a destruction of foragers, the younger individuals may leave their nursing or food storing tasks to fill the vacant jobs. This homeostatic response may be accomplished in different ways by different species.

The ways in which information about the needs of the whole colony, say for more nurses or more foragers, gets transmitted through these systems depends on a host of individual properties and coordination of activity. For example, individual bees modulate their foraging behavior based on the colony's need for nectar. How does the individual bee "know" how much nectar is needed? The amount of stored nectar is correlated with the waiting time experienced by returning foragers. That is, if the colony has a lot of nectar the receiving bees will take longer to find an empty cell in which to deposit each new load, and the returning foragers will have to wait longer to be unloaded than if there are many empty cells. If a forager has to wait a long time, then she will not be as likely to continue foraging. Here the homeostatic response of the colony is accomplished by individual bees continuing or failing to continue to forage, where the information of colony need is conveyed through the waiting time to unloading nectar. This same type of mechanism coordinating behaviors of two castes on the basis of searching time may also be involved in nest construction by paper wasps, and food collection by fire ants (Seeley 1995; Seeley and Tovey 1994).

The standard account of the ordered complex pattern of division of labor has been an adaptationist one (Wilson 1971). That is, the patterning of work within a colony is analyzed to determine what would be optimal in terms of ergonomic efficiency. If other than the optimal patterns had been exhibited in the past, they would have lost out in the competitive struggle of natural selection operating at the colony level on heritable variation. Thus the optimal variant, i.e. an age-related organization with individual specialization, would become stabilized by natural selection sorting out inferior arrangements.

The adaptationist explanation of division of labor 'black boxes' the mechanisms by which the pattern is generated. It ignores, if you like, the physiology or development of the colony phenotype. By so doing, it implicitly assumes that however a phenotypic trait may come to be expressed, as long as it is heritable, natural selection would be able to optimize on variations of that trait. However, how a trait develops can and does restrict the range of adaptive explanations that could be plausibly entertained. In particular, self-organization models of aggregate or emergent traits provide for the possibility that natural selection alone cannot explain everything about complex traits. Self-organization models have been used to describe how microscopic physical and chemical processes give rise to macroscopic structures. This type of modeling has been extended to the domain of ethology, and has been widely applied to social insects. The basic character of self-organization models is to show how complex collective behavior can emerge from interactions of individuals exhibiting only simple behaviors, without the need for either a central organizing agent or internalized complexity in the individual compo-

nents (see Bonabeau et al. (1997) and Beshers and Fewell (2001) for reviews of work in this area). In this paper I will consider three self-organization explanations that have been developed to explain division of labor. They appeal to individual genetic diversity, hive or nest architectural structure and individual learning, respectively, as explanations of division of labor. These all challenge a pure colony level selection account, since they suggest that colony level traits like division of labor and specialization, may be, at least in part, inevitable consequences of the interactions of individuals. That is, if individuals interacting generate some features of division of labor necessarily, or in Kauffman's terms "for free" (1993), then there would be no variation on the presence or absence of these features for selection to have operated on in the adaptation history of the populations. In order to clarify the relationship among self-organization explanations and between self-organization and adaptation explanations, a brief description of the assumptions used in these models is required.

A. *Genetic diversity for threshold response*

Page and Mitchell (1991, 1998) ran simulations of honeybee colonies inspired by Kauffman's n-k Boolean network model of complex systems (Kauffman 1993). Each colony had *n* individuals who interacted with *k* others. The interactions were a subset of Boolean functions, namely those that characterize threshold functions, in which the input presented to an individual would generate a response to either forage or not forage. The model presupposed genetic variation amongst the individuals that controlled the threshold level required for response to a fixed stimulus. When presented with a given level of stimulus, the bees would self-organize into a pattern of working and resting, and by working (e.g. foraging) would change the stimulus level that would be presented to the next bee. What emerged within this simple model of an amplifying feedback process was task variation within an age caste and the tuning of behavior to colony need. Specialization occurred 'spontaneously' from mere genetic variation. The conclusion drawn was that some aspects of division of labor can arise, indeed must arise, among groups of cohabiting and mutually tolerant individuals who harbor genetic variation.

The assumptions of this model are:
1. Individuals vary genetically in their threshold of response to stimuli
2. The distribution of threshold level is random
3. Behavior moderates subsequent stimulus

A pattern of division of labor and specialization coordinated to colony need emerges in this model of self-organization.

Recently, Fewell and Page (1999) empirically tested this model by forcing individuals from a solitary ant species *Pogonomyrmex barbatus* to cohab-

itate. They compared the results on task specialization with *P. californicus*, a related, but naturally cooperative ant. They concluded, "our results provide strong evidence that task specialization is an emergent property of sociality" (p. 543). That is, task specialization among individuals is not a feature of a colony open to selection *after* sociality itself has evolved. Rather, this colony level trait emerges 'spontaneously' with group living.

B. *Foraging for work algorithm*

Tofts and Franks (1992) proposed a 'foraging for work' algorithm as the basis from which division of labor emerges (see also Bourke and Franks 1995). On this model all the individuals operate with an identical algorithm; at each step they actively seek work. If work is found in one step of a clocked interval then the individual performs the task, if not found, then it will move to another work station. The individuals are all born into one station and the work stations are organized linearly, akin to a mass-production line in a factory. After an individual has moved to the second station or beyond if no work is found, it is randomly assigned to move either upstream or downstream. What emerges from this simple set of rules, is the correlation of work load to task need. An efficient distribution of workers to task is achieved, and epiphenomenally age distribution falls out.

The assumptions here are that:
1. Individuals have the identical work algorithm.
2. Nest architecture (distance from brood pile) varies the stimulus presented.

A pattern of division of labor coordinated to colony needs and age-polyethism emerges.

C. *Learning algorithm*

J. Deneubourg, S. Goss, J. Pasteels, D. Fresneau and J. Lachaud (1987) offer yet another self-organization model by which to explain the division of labor. In this case neither genetic variation nor nest architecture drives the pattern we see, but rather it is individual learning, which operates as an amplification, feed-back mechanism. Here the model assigns an identical learning algorithm to all the individuals, but assumes asynchrony in birth of new workers. There are *n* foragers in two zones. Each individual (ant, in this model) has an assigned probability of foraging at all, and a specified probability of foraging in zone 1. At the outset, all the individuals have identical probability assignments. However, through learning and forgetting the probabilities are changed. Thus the "interplay between amplification mechanism, competition between different pieces of information and individual randomness are

the factors that generate the individual behavioral patterns and the society organization." What emerges again is a pattern of division of labor with age-polyethism. Here the assumptions are:

1. Individuals have the identical learning algorithm.
2. There is asynchrony in birth of new workers.

A pattern of division of labor, with age-polyethism emerges.

The three self-organization models provide a very small subset of the theories and explanations found in contemporary biology to explain division of labor in social insects. In addition, a variety of different factors and features are appealed to, including: physiological changes like glandular development and reabsorption, where changes in body mass are coincident with changes in task; quantity of juvenile hormone secreted is associated with tasks; colony population size and character influences foraging age; quality of available resources of nectar and pollen affects patterns of division of labor; and natural selection operates at the colony level for greater efficiency.

What the self-organization models suggest is that the phenomenon seen at the social or colony level is not necessarily determined by a genetic blueprint in the individuals, which could be optimized via colony level selection. There is no necessity to postulate an internal clock that determines which individuals engage in which tasks at what times. Rather the patterns can be generated by means of the interaction of individuals on assumption of a very few internal components – genetic diversity in threshold response, uniformity of work, or learning algorithms. With the development of theories of self-organization, the toolbox of explanatory models available is expanded. Now not only are there optimality models for adapted evolution at the various levels of organization – the 'selfish gene', the cell lineage, the individual, the kin group, the colony, and the species. In addition the phenotypic characters we seek to understand may be explained by self-organization of components of complex systems.

The obvious questions arise. How are these different explanations and different models of self-organization related? Are they mutually exclusive competitors, are they equal components of a grand unified theory, or are they compatible alternatives in a pluralism of explanatory resources?

Stratification or integration?

On Sherman's account conflict between diverse explanations should occur only within a level and not between levels of analysis. Is this correct? Self-organization models of division of labor would be located at the level of ontogeny, colony-level selection models at the level of evolution. For Sherman, no conflict should occur between them. However, self-organization

models imply that, given certain properties of the individual components, interactions in a complex system necessarily generate certain forms of order. If this is the case, then historically there would have been no variation among social insect colonies for division of labor *per se*, since any complex so structured would display this pattern. Yet the evolutionary explanation of the origin division of labor appeals to colony level selection for energy efficiency and thus must, by definition, presuppose a history of heritable variation between colonies for such a pattern. Some posited answers at the two levels – ontogeny and evolution – are not mutually consistent. Thus, contrary to Sherman, there can be competition between levels (see Figure 1). Solutions to questions at one level, the developmental, affect the set of possible solutions at another level, the evolutionary. There are two different ways in which this could occur. On the one hand, developmental explanations might limit the range of viable variations that can be postulated for natural selection to have sorted between. Thus natural selection could not fashion any logically possible response to an environmental 'problem' but only those that meet the developmental constraints. On the other hand developmental theories might discover structural necessities or universals. This implies not just a limit on the range of variants under selection but an absence of variation itself. If so, then natural selection could not be the sole causal agent by which to explain the presence of the trait we now see. A well-known example for this type of constraint on possible morphological evolution is found in Murray's reaction-diffusion model. Contesting the claim that every feature of the morphology of an animal is explicable by an optimizing adaptation history, Murray's work showed that the chemical diffusion of melanin in the cells entails that it is developmentally possible for a spotted animal to have a striped tail but not possible for a striped animal to have a spotted tail (see Murray 1988; Oster and Murray 1989). Certain options are chemically precluded and hence cannot have played a role in a selective history of coat coloration. Thus evolutionary and developmental explanations can be related in ways that make knowledge of the answer to one type of question necessary to answering another type of question. The levels of analysis model masks this interrelatedness.

The other implication of Sherman's framework is that competition among explanations rightly occurs within a level. Thus we would expect that the three self-organizational models, all located at the ontogenetic level, would be mutually exclusive alternatives. But are they? I think not. An explicit feature in each of the models is the focus on a single causal factor and the exclusion of other possibly contributing causes. The different models of self-organization are idealized abstractions from the actual, complex phenomenon of division of labor (see Figure 2). That is, the genetic model of Page and

Levels of Analysis	Integrative Pluralism
Can Colony-level natural selection (evolutionary level) conflict with self-organization model (ontogenetic level) explanation of division of labor?	
NO	YES
Can genetic, architecture, and learning models of self-organization (all ontogenetic level) conflict in explaining division of labor?	
YES	NO

Figure 1. Where conflict occurs.

Mitchell ignores all factors but individual genetic diversity for threshold response for foraging. In effect, it accurately describes only ideal cases where those simplifying assumptions hold true, but only partially captures actual cases that are not ideal in this way. So, too, for Tofts and Franks's foraging for work algorithm and Deneubourg et al.'s learning algorithm. As Deneubourg et al., state "The mathematical model presented takes only learning into account, and ignores all other factors, such as age or genetic differences, which could be involved in the foraging patterns. This attitude is justified on the one hand by lack of data and on the other hand in that we wish to understand the role and limits of learning as a mechanism contributing to an insect society's organization" (Deneubourg et al., p. 179). Contrary to what one might expect on the levels of analysis picture, the three self-organization hypotheses although located at the same 'level' of analysis do not directly compete, since they describe only what would happen in non-overlapping ideal worlds.

Cartwright and Wimsatt have highlighted the literal falsity of scientific models and theories. For Cartwright the required introduction of a ceteris paribus clause to bridge the ideal world with the actual one exhibits the partiality of our explanatory models. Indeed, some components required to explain concrete events are not represented in any scientific model. Cartwright takes these epistemological features to generate a type of pluralism in science described by a "patchwork" relationship among the various theories and models we construct to explain the world (Cartwright 1994, 2000). For Cartwright, "nature is governed in different domains by different systems of laws not necessarily related to each other in any systematic or uniform

'Any model implicitly or explicitly makes simplifications, ignores variables, and simplifies or ignores interactions among the variables in the models and among possibly relevant variables not included in the model' - W. Wimsatt, 1987

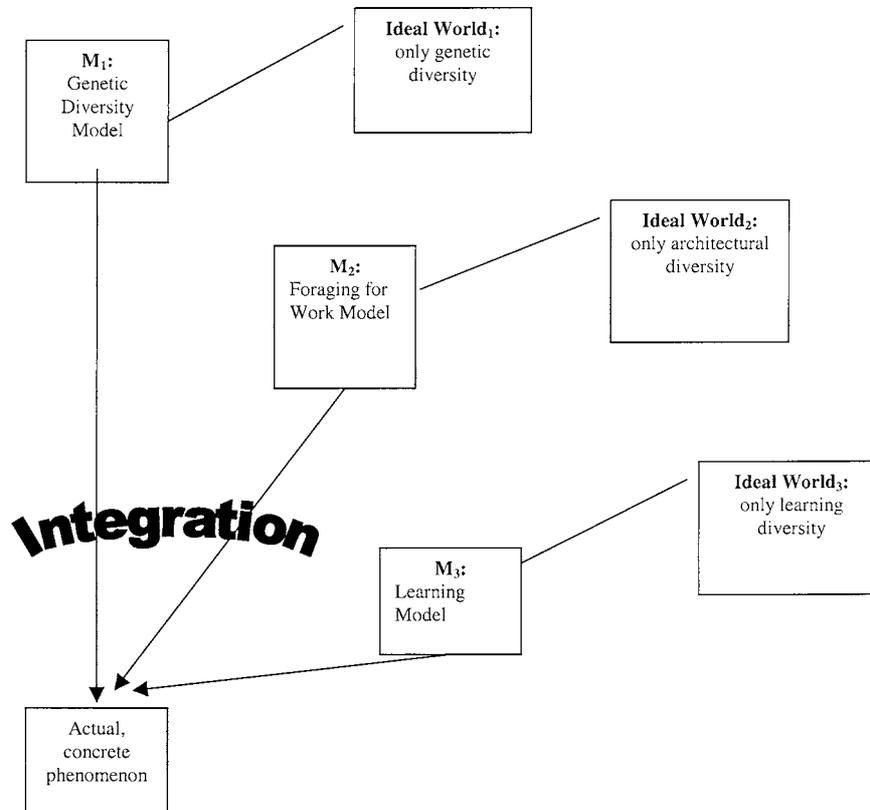'Our truth is the intersection of independent lies' - R. Levins, 1968

Figure 2. Causal models are idealizations.

way" (p. 289). Wimsatt (1987), while endorsing a similar analysis of the falsity of idealized models argues for a more dynamic solution. For Wimsatt, false models can be transformed into true theories by the addition of increasingly realistic assumptions. Thus while one might start by seeing what pattern of worker behavior would be generated by genetic diversity alone, one could subsequently combine that model with one that also included the results of learning. This second-generation model would still be ideal, but suggests a strategy of asymptotic approach to a non-idealized representation of the system. Both Cartwright's and Wimsatt's analyses make sense of a compatible pluralism of scientific models. However, I think that more can be said about the relationship of the different constituents of that pluralism

than Cartwright's patchwork image suggests. While Wimsatt's increasingly realistic model coupling strategy does articulate a more specific type of relationship among models, I believe it is only one way in which different explanatory components might be integrated.

Integrative pluralism

I have argued that the levels of analysis taxonomy in terms of different questions and correspondingly different answers failed to identify the location for competition. What then forces choices between different explanations? The answer, I believe, lies in the distinction between the theoretical modeling itself, and the application of any model or models to the explanation of a particular, concrete phenomenon. This is particularly significant in the explanation of complex structures whose features are the result of multiple causes and reflect contingent histories. As we saw above, at the theoretical level, pluralism is sanctioned. Different idealized models do not directly refer to the same ideal systems. At the concrete explanatory level, on the other hand, integration is required. However complex, and however many contributing causes participated, there is only one causal history that, in fact, has generated a phenomenon to be explained. Return to the case of division of labor. In honeybees, the queen mates with up to seventeen different drones, thereby producing genetic diversity among the workers in the colony (Page 1989; Page and Robinson 1991). The hive itself is concentrically structured with the brood in the center and storage cells further out and the entrance for foragers at the extreme edge. And the individuals are born at different times giving them different learning opportunities. Thus all of the conditions that the three self-organization models describe in isolation obtain in this system and each may contribute to features of the division of labor in honeybees. Currently, biologists are investigating how these, and other self-organization models might be combined in explaining social insect behavior (Beshers and Fewell 2001). In addition, the applicability of the models' assumptions to particular species and populations is beginning to be tested (Page and Fewell 1999). Is there sufficient genetic variation in threshold levels to generate variant behaviors? Does the architectural structure correlate with the behavior patterns? In addition to self-organizing mechanisms, natural selection may be presumed to act on features of division of labor that remain variable and thereby fine-tune this trait to the selective environment. For example, while genetic variability will generate some pattern of specialization, selection can operate on the degree of variability as well as the components of variability if these turn out to influence colony fitness.

If different models are perceived as partial solutions to a biological question, then one might argue that a theory of division of labor would be one that correctly unified the partial accounts. This would be to apply Wimsatt's asymptotic, increasingly realistic model building strategy. However, while integration of the partial accounts, indeed, is required for explaining a concrete particular, unification at the theoretical level is unlikely to be very robust. The reason is found in the evolved complexity characterizing the domain of phenomena studied by biology. It is the diversity of the 'solutions' to adaptive problems and the historical contingencies influencing those variable paths that preclude global, theoretical unification.

Ants, for example, exhibit division of labor similar to bees. Ant colonies, however, contain negligible genetic diversity compared to bee colonies. Thus, the theoretical constituents which would be integrated in the explanation of division of labor in ants would not be the same set as those required for the explanation of the 'same' phenomenon in bees. For ants, the genetic self-organization model of division of labor would often not apply. Even two distinct models of division of labor, one for ants and one for bees, would not capture the phenomena as Boomsma (1999) has detected in one species of ant nearly as much genetic diversity as in honey bees. Thus what in fact explains the existence and characteristics of division of labor in social insects, what appeared at first sight to be the 'same' phenomenon requiring a single explanation, will be itself contingent on the particular features and pathways that occur in each case. This does not issue in unrestrained pluralism since there will be only one 'true' integrated explanation for honeybees, and one 'true' integrated explanation for leaf-cutting ants. Competition among explanations in specific cases will and should occur. On this picture of idealized models and the contingent features upon which their applicability depends, pluralism will continue to characterize the models of potentially contributing causes, though not their integrated application in specific, concrete explanation.

Conclusion

The complexity of nature and the idealized character of our causal models to explain that complexity conspire to entail an integrated pluralistic picture of scientific practice. Complexity in the sense of the diversity of the contingent, evolved properties of biological phenomena has important implications for how we understand the relationships among the plurality of theories and explanations found in contemporary biology. I have argued that there is no reason to view all forms of scientific pluralism as embarrassments or signs of immaturity. This latter perspective rests on mistakenly interpreting alternative theories and explanations as always competing. While some of the plurality

found in biology is of this kind, many models are not competing, but are compatible. In these cases, competition still occurs, but it is generated only in the integrative application of the models in explaining particular phenomena.

In defending integrative pluralism, an image of science that makes room for compatibility, I have attempted to steer clear of two undesirable methodological pitfalls. The first is an isolationist stance which partitions scientific investigations into discrete levels of questions and their corresponding answers in a way that precludes the satisfactory investigation of any of the levels. The second is an uncritical anarchism that endorses all and any propositions. Neither of these positions correctly locates where and when competition in fact occurs between theories and explanations in biology. I have appealed to the idealized structure of scientific models, and emphasized the distinction between a model and its application to a concrete situation. While the idealized and abstract character of models allows compatibility at the theoretical level, the realistic and concrete nature of explanation entails integration and resolution. Furthermore, given the multiplicity of causal paths and the historical contingency of biological phenomena, the type of integration that can occur in the application of models will itself be piecemeal and, to varying degrees, local. The result is that pluralism with respect to models can and should coexist with integration in the generation of explanations of complex and varied biological phenomena.

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