

IS MACROEVOLUTION MORE THAN SUCCESSIVE ROUNDS OF MICROEVOLUTION?

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Abstract: Whether macroevolution is reducible to microevolution is one of the persistent debates in evolutionary biology. Although the concept of emergence is important to answering this question, it has not been extensively discussed within palaeobiology. A taxonomy of emergence concepts is presented to clarify the ways in which emergence relates to this debate. Weak emergence is a particularly helpful way to understand the hierarchical nature of biology: it captures the ways in which higher-level traits depend on lower-level processes, while recognizing that emergent traits can nonetheless provide the basis for autonomous higher-level theories. A brief review

of the biological literature suggests that geographical range size is weakly emergent. While some concepts of emergence do not block the attempt to reduce macroevolution (i.e. the attempt to explain all macroevolutionary phenomena in terms of microevolutionary processes), weak emergence does. Thus, if geographical range is weakly emergent, it provides a basis for arguing that macroevolutionary phenomena cannot be fully explained by microevolutionary processes.

Key words: emergence, downward cause, geographical range, hierarchy, macroevolution.

EMERGENT properties have gone in and out of vogue. After a period of considerable popularity during the late nineteenth and early twentieth century, the concept of emergence was dismissed by logical empiricists as ‘sloppy thinking’, only to experience a renaissance during the final decades of the last century (McLaughlin 1992). The rise of dynamical systems (‘chaos’) theory brought legitimacy to the concept of emergence and scientists began to talk more freely about emergent properties (Silberstein and McGeever 1999). These scientific developments, in turn, have prompted philosophers to reconsider the concept of emergence, so that philosophers are now writing papers with titles such as ‘The re-emergence of emergence’ (Cunningham 2000).

The concept of emergence seems to be required for the study of some domains. For instance, conscious experiences, such as the taste of lemon or the feeling of embarrassment, seem to be strikingly new and different from any of the physical properties of the brain or its component neurons. Yet somehow, when enough neurons are assembled in the right way, conscious experience occurs. Similarly, living organisms display properties, such as reproduction, metabolism and growth, that seem qualitatively different from the properties displayed by non-living molecules, even though the living being is a very complex collection of molecules. As we ascend in hierarchies of inclusiveness (studying larger objects, but without introducing any non-physical ‘elan vitale’) we encounter

novel properties that cannot be attributed to entities at lower levels and cannot, it seems, be explained as simple aggregations of lower-level properties.

Understood in this way, emergence is a form of ‘non-reductive physicalism’. Physicalists hold that all objects and events are (collections of) physical objects and events; there are no non-physical entities or properties. Nonetheless, emergentists claim that our theories about large wholes cannot be reduced to theories of parts. Theories that explain the behaviour of parts in isolation may not suffice to explain the behaviour of these complex wholes.

Emergence has been discussed in many fields, including cognitive science, chemistry, physics, artificial life/computer science and biology, but has not been discussed much within palaeontology. If palaeontologists have encountered the term at all, I suspect it is through the work of Vrba (1984, 1989). However, because Vrba’s conception of emergence is merely one of several different ways of conceptualizing emergence, it is helpful to explore alternative ways of defining it. Thus, the first goal of this paper is simply to present a range of alternative ways of conceptualizing emergence. Developing a critical understanding of alternative conceptions of emergence is particularly important when reflecting on the vexed question of how micro- and macroevolution are related.

This paper addresses three principal questions: (1) what is ‘emergence’?, (2) are any emergent traits involved in

central macroevolutionary processes? and (3) do these emergent traits (if they exist) block the attempt to reduce macroevolution to successive rounds of microevolution? After distinguishing four definitions of 'emergence', I argue that Mark Bedau's concept of 'weak emergence' holds promise as a way of understanding emergence in the macroevolutionary domain. In particular, his theory provides a natural account of why geographical range is emergent and how this form of emergence blocks attempts to reduce macroevolution. In short, recognizing that geographical range is weakly emergent bolsters the claim that there is an autonomous domain of macroevolutionary explanation.

ON THE RELATIONSHIP BETWEEN MICRO- AND MACROEVOLUTION

Whether macroevolution involves special higher-level mechanisms is one of the persistent debates in evolutionary biology. Although the specific macroevolutionary hypotheses have changed over time (e.g. orthogenesis, macromutations, quantum speciation, punctuated equilibrium, species selection, extraterrestrial causes for mass extinctions), the larger debate has persisted (e.g. Bock 1979; Gould 2002). The 'problem of macroevolution' is to understand the relationship between the micro- and macroevolutionary domains. 'Microevolution' is typically understood as evolution 'below the species level' including, but not limited to, the following processes: mutation, recombination, gene flow, drift, natural selection, local interaction among species (such as parasitism, predation and competition), and mechanisms of speciation. By contrast, the macroevolutionary domain includes phenomena at larger temporal, geographical or taxonomic scales such as the latitudinal diversity gradient, mass extinctions, long-term diversification patterns, geographical and temporal patterns in the origination of major evolutionary novelties, and patterns in the occupation of morphospace. At the time of the evolutionary synthesis, Simpson argued that the macroevolutionary patterns observed in the fossil record are 'compatible' with Neo-Darwinism. But even if macroevolution does not contradict microevolutionary theory, three different relationships between these domains could be realized.

1. Explanatory reduction of macroevolution. Although philosophers have argued about the best way to understand intertheoretic reduction, the core idea of reduction is clear enough (Schaffner 1993 and Sarkar 1998 provide literature reviews). *Explanatory* reductionists hold that more basic (lower-level) theories can do all the explanatory work of less basic (higher-level) theories, plus more besides. Thus, to say that macroevolution is *explanatorily* reducible means that microevolutionary theory can do all

the explanatory work of macroevolutionary theory. To put this somewhat differently, combining an idealized lower-level theory with the set of background conditions would (in principle) allow us to explain any given macro event. According to this reductionist view, the principal role of macroevolutionary studies is to determine empirically the 'initial conditions' (parameters) that are input into our explanations (e.g. what other species existed in that location at a given time, when a meteor hit the Earth, how the continents moved). Once palaeontology provides the parameters, micromechanisms do all the explanatory work. Thus, reductionists do not recognize any distinctive body of macroevolutionary theory because all macroevolutionary generalizations are derivative – literally. They can be derived from the microlevel theory (plus initial conditions). Because the reductionist gives preference to lower-level (genetic and population-level) mechanisms, if we assume that palaeontology has a limited ability to study micromechanisms, then the empirical study of macroevolution (especially through the fossil record) will not advance our understanding of evolutionary mechanisms. Even if palaeontology has some distinctive knowledge (e.g. taphonomy) and methods for studying fossils, the crucial mechanisms (causal processes) for explaining evolution occur at lower levels and are best studied in living organisms.

2. An intermediate possibility. An intermediate possibility grants greater significance to the study of macroevolution while still accepting 'in principle' reduction. On this view, macroevolution needs to be studied in its own right because, in doing so, we are led to revise the expectations derived from lower-level theory and data. But ultimately, one might argue, the macro-patterns are best explained by appealing to complex combinations of lower-level processes. As a result, this intermediate possibility is compatible with 'in principle' reductionism. This second scenario differs from the first because it highlights (as reductionists usually do not) ways in which higher-level study is crucial to the advancement of the field. In other words: we cannot simply 'reduce' macroevolution to *existing* claims about how microevolutionary processes combine. Both the lower- and the higher-level theories are in flux, driven partly by the data discovered in studying macroevolution.

3. Distinctive (irreducible) macroevolutionary mechanisms. The clearest way to validate macroevolution as a domain of study is to demonstrate that there are irreducible macroevolutionary processes. The best known candidate is species selection (see, e.g., Grantham 1995, 2002). A hierarchically expanded evolutionary biology is 'compatible' with and incorporates the evolutionary processes described by population genetics, but denies that the microevolutionary catalogue of processes is *complete*.

Of these scenarios, the third gives macroevolutionary studies the greatest significance and autonomy, arguing

that macroevolutionary *mechanisms* are worthy of study in their own right, not simply the long-term aggregation of microlevel processes. This is where ‘emergence’ is poised to make a difference. If some causal processes operate on properties that emerge at the species, clade or community levels, then there may be distinctly macroevolutionary processes that cannot be explained in lower-level terms. One important obstacle confronting advocates of this third position is to explain how it is compatible with physicalism. To address this worry, one needs to distinguish ontological and epistemological reductions.

Physicalism holds that there are no non-physical entities or properties: that no supernatural entities exist. If physicalism is true, then every higher-level object must be a (complex) combination of smaller physical things. *Ontological reductionists* maintain that if physicalism is true, then we can *define* higher-level entities and properties in lower-level terms. Although this thesis may seem plausible at first, it has not withstood philosophical scrutiny (e.g. Fodor 1974; Kincaid 1990). Within philosophy, physicalists have largely abandoned the more demanding notion of reductionism in favour of ‘supervenience’. According to this latter notion, higher-level entities and properties depend on lower-level properties, so that a different higher-level property cannot differ without a lower-level difference. [Philosophers have distinguished several different notions of supervenience (McLaughlin 1995); for our present purposes I will focus on the notion just given, which is called ‘global supervenience’ in the literature.] To distinguish this current position from earlier (reductionistic) claims, I will use the phrase ‘ontological dependence’ to describe an ontological stance committed to physicalism and supervenience, without presupposing that it is possible to define higher-level traits in lower-level terms. To say that macroevolution *ontologically depends* on microevolution, then, would mean that the macroevolutionary domain is a strictly physical domain (no supernatural or magical properties), that each macroevolutionary entity and property supervenes on microevolutionary entities and properties, and that the behaviour of these higher-level entities is causally determined by these lower-level entities and properties.

As a form of non-reductive physicalism, emergentism claims that even if we accept that macroevolution *ontologically* depends on microevolution, it may not be *explanatorily* reducible. If some macroevolutionary processes operate on emergent properties at or above the species level (e.g. species lineages, clades or ecological communities) then macroevolution may be explanatorily irreducible. A full understanding of the macroevolutionary domain will require reference to these processes that cannot be understood in solely microevolutionary terms.

How we solve the problem of macroevolution, then, has important ramifications for the role of palaeontology

within evolutionary biology. Palaeontology’s main contribution to evolutionary biology is its ability to document large-scale (macroevolutionary) patterns in the history of life. If explanatory reductionism is true, the study of macroevolution will not strongly shape evolutionary theory. Rather, palaeontology merely applies theories given ‘from below’, with all the real causal/explanatory work being done at lower levels (e.g. Gould 1980). While the second option gives palaeontology a worthy role within evolutionary biology, only the third scenario (irreducible explanations) ensures that macroevolutionary phenomena are not just complex summations of lower-level causes. Thus, palaeontologists should have an abiding interest in whether the macroevolutionary patterns they study are best explained by appeal to emergent properties that would block an explanatory reduction.

Emergent traits may not be the only way to have irreducible explanations. For example, it may be possible to have species selection without emergent traits (Grantham 1995). But the discovery of emergent traits would certainly make it easier to demonstrate that there are distinctive (irreducible) macroevolutionary explanations.

CONCEPTS OF EMERGENCE

Many different kinds of things have been called emergent: phenomena, levels, laws, properties and dynamics. Life and consciousness have been treated as emergent phenomena. Arguably, Maynard Smith and Szathmari’s (1995) ‘major transitions’ correspond to emergent levels: each transition creates a new way of organizing lower-level materials so that the newly evolved systems display novel properties and obey qualitatively different (emergent) laws or generalizations. Organisms are said to have emergent properties that cannot be attributed to lower levels of organization (cells, tissues or organs); higher-level entities (such as populations, colonies and species) may have emergent traits, as well (e.g. Gerard *et al.* 2002; Cassill 2003). While even this brief list shows the diversity of phenomena treated as emergent, it is helpful to focus on the emergent properties. Once we can identify emergent properties, it will be relatively straightforward to apply the concept in other contexts (e.g. an emergent law is a law about an emergent property). This section presents a taxonomy of several emergence concepts. My classification is largely borrowed from Bedau (2002; see Cunningham 2000 for an alternative taxonomy).

Emergentists are typically committed to two theses. First, as physicalists, they believe that macroproperties ontologically depend on the micro-realm, as described in the last section. Second, as non-reductionists, they believe that our theories about macro-entities and properties are,

in some way, autonomous from our theories about the micro-realm. Although emergentism rejects *metaphysical* dualism (i.e. the claim that there are non-physical entities or properties), it does embrace a form of *explanatory* dualism in which distinctive higher-level theories and explanations are scientifically legitimate and necessary to explain fully the domain of phenomena. By varying the ways in which these dependence and autonomy relationships are conceptualized, we can arrive at substantively different conceptions of emergence.

Nominal emergence. Some terms simply cannot be applied to lower-level entities. For example, sex ratio (ratio of male and female organisms) is a property of populations, not of organisms. (NB: a single monoecious plant can, however, display a ratio of male to female reproductive parts.) Elisabeth Vrba has emphasized nominal emergence: 'an emergent character is a structural or dynamic character that is level-specific in that it does not exist at any lower level' (Vrba 1989, p. 113). Or again: 'Such characters cannot be said to be properties of any entities at lower levels, but emerge at the focal level' (p. 131). The intuitive picture driving this definition is that biologists study systems of nested entities such as genes, cells, organs or organisms. Some properties (such as 'mass') occur at all levels. Others make their first appearance at higher levels. For example, the number of forelimb digits is emergent at the organism level because it is not a property of genes, cells or tissues. Regarding macroevolution, the propensity to speciate emerges at the level of lineages and trophic structure emerges at the level of communities.

Non-aggregativity. Wimsatt (1997) regarded all non-aggregative traits as emergent. Roughly, this means that if the property of the whole depends on the way the components are organized, then the higher-level property is emergent. More precisely, aggregativity requires that three conditions be met: (1) it is possible to decompose and re-assemble the system in any way and the higher-level trait remains fixed; (2) there are no co-operative or inhibitory interactions among the parts; and (3) adding or subtracting parts does not qualitatively change the behaviour of the system. This analysis differs significantly from Vrba's. In fact, nominal emergence is neither necessary nor sufficient for non-aggregativity. Consider a table that can be decomposed into, say, 13 parts (four legs, a top and eight screws). According to Vrba, 'height' is not nominally emergent because all of the pieces have a height. Nonetheless, height is non-aggregative because the height of the table depends on how the various parts are organized. Thus, nominal emergence is not necessary for non-aggregativity. Or consider sex ratio, again. If we treat organisms as the 'parts' of the population, then sex ratio seems to be aggregative: we can decompose the popula-

tion and re-compose the population without altering sex ratio. But because sex ratio is nominally emergent, nominal emergence is not sufficient for non-aggregativity. [The claim that sex ratio is aggregative concerns synchronic emergence, the relationships between parts and whole at a given time slice. If we focus, instead, on the dynamics of sex ratio evolution, then sex ratio will probably emerge (i.e. be non-aggregative) at the population level because its evolution depends crucially on population structure.]

Neither nominal emergence nor non-aggregativity is sufficient to block explanatory reduction. Vrba (1984, p. 324) recognized that her concept does not block reductive explanations. For example, even though sex ratio is *nominally* emergent at the population level, it can be determined (at any given moment in time) by studying the organisms in isolation. Furthermore, sex ratio may be reducible diachronically if, for example, we can explain changes in sex ratio over time by appeal to selection at the level of organisms and other standard microevolutionary processes. Thus, nominal emergence (by itself) does not block the reduction of macroevolutionary phenomena. Wimsatt (1997) regarded it as a virtue of his analysis that his notion of emergence is compatible with reductive explanation. Aggregativity fails when the system-level property depends crucially on the spatial organization or non-linear interaction of parts. But if we can explain these non-linear interactions in terms of a lower-level theory, then we will be able to provide reductive explanations for emergent traits. Wimsatt's account has real appeal: it identifies a crucial aspect of emergence, namely, the sense that the emergent property arises out of (non-aggregative) interaction among the parts. In addition, non-aggregativity allows us to recognize that emergent phenomena can be explained as the result of lower-level interactions. However, if we are looking for a concept of emergence that might block the claim that macroevolution is just a summation of microevolutionary processes, Wimsatt's theory will not help.

Strong (ontological) emergence. Strong (ontological) emergence challenges the ideas of physicalism and/or supervenience. One version of strong emergence holds that 'emergent properties have causal powers of their own – novel causal powers irreducible to the causal powers of their basal constituents' (Kim 1999, p. 22). Kim (1992, 1999) argued that this particular formulation of downward causation is incoherent. Emergentists believe that higher-level properties must be realized by a set of lower-level entities (and their properties). To say that this property is 'realized' by a set of lower-level properties means that, in this particular instance, the higher-level property (H) is nothing more than a set of lower-level objects L (and their properties) organized in a particular

way. For example, fear is a complex state of one's neural system. Higher-level traits are often 'multiply realizable', meaning that many different lower-level states can produce the same higher-level state. For example, different individuals' brains may realize 'fear' differently (either within a single species or across different species). But each instance of fear will be realized by a brain state. Similarly, many different combinations of organismic and population-level properties (e.g. genetic and population structures) can yield the same propensity to speciate or the same geographical range. The problem with downward causation is just this: assuming that the emergent property H1 is realized by a lower-level state L1, how could H1 have any causal powers over and above the powers of L1? That does not seem to be possible, or at least it seems to violate physicalism. Thus, the notion of emergence faces a dilemma: either we give up physicalism (in which case emergentism ceases to be a form of non-reductive physicalism) or we give up the claim that emergent traits have distinctive causal power. This way of conceptualizing 'downward causation' is, then, metaphysically problematic. (In the discussion I will argue that weak emergence can support autonomous levels of explanation without appealing to such controversial metaphysics.) Furthermore, although ontological emergence may be plausible for certain physical phenomena (see Silberstein and McGeever 1999) few biologists are tempted towards it (Boogerd *et al.* 2005). The plausible cases of emergence in biology seem not to require any violation of physicalism or supervenience; emergent traits such as sex ratio and geographical range depend on lower-level traits and do not have causal powers that differ from their lower-level realizers.

To summarize our results so far: nominal emergence and non-aggregativity do not (by themselves) establish that macroevolution is irreducible. By contrast, strong ontological emergence (such as downward causation) would guarantee irreducibility but appears to be metaphysically or biologically implausible. In the last few years, several philosophers have tried to develop intermediate theories to plug this gap. Following Bedau (1997, 2002), I call these 'weak emergence' theories.

Weak emergence. Weak emergence combines ontological dependence with 'explanatory autonomy'. According to this conception, higher-level properties supervene on the set of lower-level 'base' properties so that the higher-level properties cannot vary unless the lower-level properties vary. Although the higher-level traits are determined by the lower-level traits, a fully satisfactory theory requires causal generalizations about higher-level properties. This middle ground strikes some as an attempt to have one's cake and eat it too: if we accept an ontological dependence relationship in which the causal powers of higher-

level entities are determined by lower-level phenomena, how can we get any significant sort of *explanatory* irreducibility? This core problem will be addressed in the discussion. It is first necessary to articulate Bedau's concept of weak emergence more fully and see how it might apply to the concept of geographical range.

Bedau (1997, 2002) has articulated a theory of weak emergence, focusing specifically on the behaviour of computer models such as 'the game of life'. In these models, the state of the game at any time supervenes on (and is completely determined by) the microstate of the system. He has argued that even when supervenience and causal determination obtain, emergent properties can provide a platform for explanatory autonomy. One aim of this paper is to show that his analysis, initially developed by studying computer models, can be fruitfully applied to empirical domains.

According to Bedau (2002), property P is weakly emergent at level L if and only if: (1) P is globally supervenient (the macro property is realized by an arrangement of sub-L entities/properties); (2) the exact value of P is derivable from a description of microfacts only by full simulation; (3) P is crucial to the statement of robust causal generalizations; and (4) P is nominally emergent at L. (Strictly speaking, Bedau said that conditions 1, 2 and 4 define 'weak emergence'; adding condition 3 leads to 'robust' weak emergence. I focus on the robust concept because it is poised to block reduction.) The first two clauses correspond roughly to my concept of ontological dependence. The third and fourth clauses provide a basis for explanatory autonomy. One crucial point is that P cannot be predicted from the lower level without simulating the full suite of processes that have historically led to P. In other words, the dynamical processes that determine P are 'causally incompressible' (M. Bedau, pers. comm. 2005). This account of weak emergence does allow for a kind of reducibility. The precise value of P can, in principle, be explained by tracing out the full causal sequence of lower-level events that led to P. In this respect, Bedau's weak emergence resembles Wimsatt's non-aggregativity. Nonetheless, if there are robust generalizations about P, i.e. if P itself is crucial to an adequate description of higher-level mechanisms or causal processes, then we cannot reduce those higher-level mechanisms (processes). Let me elaborate.

Requiring that the process is causally incompressible means that there is no lower-level 'short cut' to predicting the value of P. When incompressibility is combined with the fact that P is causally salient (i.e. crucial to the statement of a causal generalization or explanatory model), irreducibility follows. To see this, first consider what happens when there is a causal 'short cut'. Suppose, for instance, that given full information about the initial conditions and selective forces operating on a large

population, we can accurately predict the equilibrium sex ratio of a population without tracing out its full causal history. Even if sex ratio has further causal effects, it is not unreasonable to view the causal chain 'organismic selection regime \rightarrow sex ratio \rightarrow effect' transitively, so that further effects can be explained reductively as a consequence of organismic selection. Essentially, the organismic selection regime provides a 'proxy' for sex ratio (at least within a certain range of conditions) so that we can explain the effects of sex ratio as remote effects of this selection regime. If, by contrast, the emergent trait is both causally incompressible and causally salient, then its causal role (the second causal arrow) cannot be 'reduced'. Both the reducible and the irreducible scenarios involve supervenience, nominal emergence and give sex ratio a causal role; the crucial difference is the way in which lower-level processes produce the emergent trait. When these processes are so complex that we cannot provide short-cut explanations of the occurrence of P, then we are required to recognize P as having causal significance of its own. Here is another way to see the point. An indefinitely large set of lower-level realizations could produce this value of P, but the precise lower-level realization which occurs does not (causally) matter. All that matters (from the vantage of understanding the mechanism of the second causal arrow) is the value of P. This abstract point will become clearer when applied to geographical range, below.

Boogerd *et al.* (2005) offered a different way to understand explanatory autonomy. Like Bedau, they accepted that given a full lower-level description of all the parts, their relationships to one another, and the environment, we can determine the higher-level property at that time. But there is still a kind of explanatory autonomy: if we were to study the parts in simpler wholes, we would not empirically or theoretically be able to discover how they would interact in a more complex whole. Of course, once we have studied complex wholes, we will understand how they behave. Nonetheless, lower-level research (i.e. on parts in isolation or in less complex wholes) would never allow us to understand how the wholes would behave. (Boogerd *et al.* called their view 'strong' emergence but it is very similar to Bedau's 'weak' emergence.) Although Bedau's theory of weak emergence is helpful for understanding why geographical range is emergent, other ways of conceptualizing emergence may be fruitful when studying other empirical domains.

How does weak emergence relate to the concepts discussed earlier? As explained below, geographical range is weakly emergent at the species level, even if it is nominally emergent at the population level. Thus, weak emergence at a given level does not require nominal emergence at the same level. The relationship between non-aggregativity and weak emergence is much closer. Although non-aggregativity is not sufficient to guarantee

explanatory autonomy, failures of aggregativity are crucial to my account of why geographical range is emergent. In fact, to the best of my knowledge, all cases of weak emergence presuppose some form of non-aggregativity. Thus, weak emergence is compatible with nominal emergence and non-aggregativity. However, because strong emergence tends to reject the claim that higher-level causal powers are causally determined by lower-levels, strong and weak emergence are not generally compatible.

Another way to appreciate the close relationship between nominal emergence, non-aggregativity and weak emergence is to realize that some candidates for emergent traits in macroevolution very likely satisfy all three conditions. Consider, for example, evolvability and the propensity to speciate. These traits nominally emerge at the species level and are probably non-aggregative and weakly emergent; because they depend on a large number of lower-level causes that interact in non-linear and context-sensitive ways, the dynamical process will be causally incompressible. Or, to take a more ecological example, aspects of community structure (e.g. trophic structure) may very well be emergent in all three senses. If these three concepts overlap to this extent, why regard the concept of weak emergence as so special? Weak emergence has special utility because it clarifies how emergent properties can block reduction, something the other concepts do not offer. And that, we have seen, is important in resolving questions about the relationship between micro- and macroevolution.

BIOLOGY OF GEOGRAPHICAL RANGE SIZE

The concept of geographical range is central to several active research fields within ecology and evolutionary biology. Because species that are restricted to small geographical areas are at higher risk of extinction, geographical range is a crucial concept within *conservation biology*. It now appears that the shape and structure of the range, in addition to the total area covered, influence extinction risk (Brown *et al.* 1996). The central problem of *biogeography* is to explain the mechanisms that govern the distribution of species across the globe. Similarly, *macroecology* aims to explain large-scale ecological patterns, including several patterns that involve the distribution of geographical ranges (Brown 1995). Finally, because it is one of the few plausible candidates for an emergent species-level trait capable of driving macroevolutionary trends, geographical range has been central to the debate about the *hierarchical expansion of evolutionary biology* (Grantham 1995). Thus, geographical range plays an important role in macroevolutionary and macroecological explanations.

Geographical range is, at base, the total geographical area over which a species is present. Though simple in concept, range is not easy to put into operation. The precise location of range boundaries will depend on the spatial resolution (grid size) of our maps, the abundance level required to count a species as present at any given area, and the time period over which measurements are taken (because range boundaries move). Furthermore, once the outer boundaries for the range are set, one must consider how to address lacunae where the species is absent within these outer limits. (Gaston 2003 distinguished between the extent of occurrence, the total range falling within the species' outer boundaries, and the area of occupancy, which includes only the area occupied by populations.) Finally, range size can only be determined after species are classified: we must know whether we are dealing with one widespread species containing two subspecies or two geographically separate sister species in order to determine geographical ranges correctly. For the purposes of this paper, I assume that we can develop reasonable methods and conventions to address these issues.

According to many models of speciation, the majority of newly created species will occupy a relatively small range. (Speciation by vicariance is one important exception.) At the time of extinction, range goes to zero, but in the period between speciation and extinction, a species' range can expand or contract. These processes (speciation, extinction, range expansion and contraction) generate the tremendous diversity of range sizes. Some species, such as the blue whale and some seabirds, range across nearly all oceanic environments. At the other extreme, some species are endemic to small islands. The entire distribution of ranges covers 12 orders of magnitude, from less than 100 m² to over 300,000,000 km² (Brown *et al.* 1996). Within taxonomic assemblages, geographical ranges typically have strongly right-skewed distributions when measured on non-log axes (Gaston 1998). What explains this variation in ranges? Why are some species so widespread, while others are so narrowly restricted?

A wide variety of factors are known to influence geographical range (see reviews by Brown *et al.* 1996; Gaston 2003). (1) *Physical barriers*: many features of the physical environment can prevent species from spreading (e.g. mountains and bodies of water). (2) *Climatic barriers*: even without obvious physical barriers to dispersal, a species may not be able to spread to neighbouring environments; for example, some species are unable to spread to higher latitudes because they cannot tolerate winter temperatures. (3) *Organismic capacities*: physical and climatic features become *barriers* only relative to the capacities of organisms; for example, a mountain might provide a serious barrier for a plant species that cannot survive at high elevation and has low dispersal capacity; by contrast, the same mountain may not provide a significant barrier to a

wind-dispersed plant that can survive at higher elevations. Examples of organismic traits that influence range include niche breadth (such as range of food items consumed), environmental tolerance and dispersal ability. For example, contrast a species that is narrowly adapted to feeding on one plant with a generalist species. The former will be limited to that plant's range; a less specialized species can, other things being equal, spread more widely. Similarly, if the organisms in one species are capable of wider dispersal, then those organisms are (other things being equal) more likely to find and colonize new localities to which they are suitably adapted. One well-known example concerns the mode of development in molluscs. Molluscs with prolonged development, where the larvae spend a considerable time in the water column, can disperse widely. By contrast, species that settle out of the water column more quickly have much lower dispersal capacity. A body of evidence shows that mode of development affects dispersal and, ultimately, the geographical range of the species (e.g. Jablonski 1986). However, a species with a high intrinsic capacity to spread may not achieve a large range if it is bound by physical barriers. (4) *Interspecific interactions*: interspecific competition, range limits of host plants, predation and parasitism can all limit a species' range. (5) *Population dynamics*: even if organisms can successfully disperse to an environment and can survive there, there may be obstacles to establishing a breeding population successfully; thus, population dynamics can also create barriers to long-term range expansion (e.g. Lennon *et al.* 1997).

Geographical range is a significant species-level property because it is correlated with (and probably causally related to) a number of important variables, including latitude, body size, abundance and species longevity (see Gaston 2003). The precise relationships among these variables are complex and not yet fully understood. I will focus on the relationship between range and extinction risk (or its inverse, species duration). As Gaston (2003) pointed out, the evidence supporting this relationship is not, perhaps, as strong as one might like. For instance, the correlation between 'threatened species' and species with small range is merely tautological if we use small range as one criterion for determining which species are threatened. Nonetheless, data from many different taxonomic groups suggest that extinction risk is correlated with range size (Purvis *et al.* 2000; Jones *et al.* 2003; Jablonski and Hunt 2006). Initially, some authors worried that the observed correlation between range and duration among fossil taxa might be a preservational artefact. However, Jablonski (1988) and Marshall (1991) have shown that the preservational bias is not sufficient to explain the observed patterns.

For the purposes of this paper it is not necessary to address the question of whether range size is heritable at

the species level (Webb and Gaston 2003, 2005; Hunt *et al.* 2005; Jablonski and Hunt 2006). Range size can be dynamically emergent whether or not it is heritable. Whereas range size can be *emergent* without being heritable, true species selection for range would, of course, require heritability.

GEOGRAPHICAL RANGE IS WEAKLY EMERGENT

To show that geographical range is weakly emergent (in Bedau's sense) and sufficient to block the reduction of macroevolution, four points need to be established. Geographical range must be: (1) ontologically dependent on organism- and population-level properties (i.e. supervenient upon the lower-level entities/properties and dynamically determined by lower-level causal processes); (2) causally incompressible (derivable only by simulation); (3) causally salient (crucial to the statement of robust generalizations, mechanisms or causal processes); and (4) nominally emergent at the species level. Let us address each criterion in turn.

1. Although the biology of geographical range is not fully understood, it is reasonable to assume that geographical range supervenes on lower-level entities and properties. Thinking synchronically (i.e. about the relationship between a species and its members at a given time-slice), the range of the species is determined by the physical location of the organisms that belong to that species. It is important to note, however, that this involves more than specifying the *intrinsic* (non-relational) properties of the organism; the *location* of the organisms must also be specified, which is really a relationship between the organism and its environment. Proof: we could take a set of organisms, without altering their intrinsic properties, and move them around so that they occupy a smaller or larger range. Thus, geographical range does not supervene solely on the intrinsic properties of organisms.

Now consider how the range of a species changes *dynamically* over time. As explained in the previous section, physical barriers, climatic/niche limitations, organismic properties, interspecific interactions and meta-population dynamics all influence range. The crucial question, for the present purposes, is whether these causal factors are all 'lower-level' causes. As I explained earlier, standard models in population genetics and population ecology (including selection and local interspecific interactions) count as lower-level processes. Given this rough understanding, the organismic properties and interspecific interactions should be understood as 'lower level'. Note, in particular, that if we regard macroevolution as a process at or above the species level, then dispersal and meta-population dynamics are 'micro', even though they are

not 'within-population' processes. Barriers and climatic limitations pose a challenge because they involve 'macro' features of the environment. Although oceans and mountain ranges are clearly 'macro' features of the environment, it is possible to maintain that the causal processes all involve lower-level interaction. Consider the well-known phenomenon of isolated populations occurring at higher latitudes than a species' normal range. This happens because the population occupies an atypical local habitat (e.g. one that is unusually warm for that latitude). Thus, the crucial causal factor is not the typical climate at a given latitude, but the actual *local* environmental conditions. Similarly, a local population interacts with a macro barrier only by interacting with some *local* part of the barrier. Assuming that it is reasonable to regard such local interactions as being covered by microevolutionary theory, these reflections suggest that the geographical range is (dynamically) causally determined by lower-level causal forces. (Note that the 'base' of the dynamic account is larger than the base for the synchronic supervenience discussed in the previous paragraph: in addition to intrinsic and relational properties of organisms, we must also include a rich account of the physical and biotic environment, including changes in the environment over time.) In other words, geographical range is dependent upon lower levels (both ontologically and causally). But if range is both ontologically and causally so dependent upon lower levels, in what sense is it emergent?

Bedau argued that dependent traits can still be weakly emergent if they are causally incompressible and function crucially in robust causal generalizations. Here is how it might work. Although geographical range is causally determined by lower-level causes, these causes are often so complex that the precise range of a species could not be predicted except through full simulation. Furthermore, range *per se* (not its lower-level determinants) is causally or explanatorily salient. When these two conditions are met simultaneously, range blocks the attempt to reduce macroevolution because there are higher-level causal generalizations (about the relationship between range and extinction risk) that require us to refer directly to higher-level properties. Does range satisfy these two criteria?

2. In some conditions, at least, range is dynamically incompressible. This incompressibility arises from the fact that range size depends on many different aspects of the organisms' biology, is context-sensitive and is often non-linear, so that small changes in initial conditions can lead to large changes in system behaviour. Gaston (2003, p. 51) argued that geographical range involves multiple causal factors: 'in any particular area, and at any given time, the distributional limit of a species may be mediated by complex interactions between factors.' Furthermore, the factors that limit a single species can vary spatially (if different factors are limiting for different

range boundaries) and temporally (as the species or the environment changes). Even the members of the species generally vary systematically across the species' range because of local adaptations. It is reasonable to assume that, at least in some cases, this suite of causal dependencies will be strongly historically sensitive. Consider, for instance, how sea-level changes have periodically blocked movement across the isthmus of Panama. Suppose a species is expanding its range southward while sea-level is rising; if it had expanded more rapidly, it might have been able to cross the isthmus and significantly enlarge its range. Incumbency effects (where established species prevent range expansion) also create historical sensitivity (Sheehan 2001). Finally, some of these relationships are likely to be non-linear. For example, depending on the physical geography, small changes in dispersal ability or environmental tolerance may allow a species to expand beyond a barrier. Similarly, models of meta-population dynamics often show crucial thresholds below which viable populations cannot be maintained (Lennon *et al.* 1997). Because range is a product of many factors that interact in non-linear and context-sensitive ways, the dynamics of range growth and contraction will generally be causally incompressible. The attentive reader will have noted the caution of this last statement. I do not claim that range is always incompressible. There may be circumstances in which one or a few organismic traits drive range expansion so that the resulting range is not sensitive to small changes in the initial conditions or the historical sequence of events. In these cases, the dynamical behaviour of the system will be predictable from a small set of micro-level causes and the explanatory autonomy will fail. Thus, range may not always be weakly emergent at the species level.

3. The third condition, that range is crucial to robust explanatory or causal generalizations, is an empirical claim. Consider the claim that large range reduces extinction risk. Although this relationship has not been definitively established, it is highly likely given what we currently know about the biology of geographical range. Many authors regard large range as one factor that prevents extinction (e.g. Purvis *et al.* 2000; Gaston 2003; Jablonski and Hunt 2006). The issue is whether range is actually a distinct causal factor or is merely correlated with longevity. Although there is not a large body of data to support the claim that range has causal force over and above other lower-level causes, it is reasonable to suppose that it does. At least with respect to some factors that drive extinction (e.g. rapid environmental changes), small range itself would contribute to higher extinction risk. If a species has a small range and that entire range becomes (even temporarily) uninhabitable, then the species will go extinct. Jablonski and Hunt (2006) have used Brandon's (1990) 'screening off' test to argue that range is an

important factor, over and above organismic factors. Here is the idea: because adding range to a set of (lower-level) causal factors leads to more accurate predictions of extinction risk than those lower-level factors alone, range probably has causal significance apart from those lower-level factors. Similarly, Jones *et al.* (2003) found that range size is the single best predictor of extinction risk in bats.

4. Although geographical range fits Bedau's analysis well, it seems to violate the fourth condition. Bedau (2002) stipulated that for a trait to be weakly emergent at a level, it must be nominally emergent at that level. Arguably, however, geographical range arises at the level of populations. Consider a species that exists as a single population. In this case, species range is identical to population range. Thus, populations must have a range, making range nominally emergent at the population level. Thus, applying Bedau's theory to a more empirical domain teaches us that nominal emergence at level L is not strictly necessary for weak emergence at L. When viewed synchronically, a species' range may closely approximate an aggregate property (simply sum up the range of each geographically non-overlapping population, ignoring the fact that populations may be specially adapted to local conditions), but it is still dynamically incompressible. Furthermore, *species* range seems to be salient for extinction resistance. Thus, even if range nominally emerges at the population level, it appears that *species-level* range has irreducible causal significance.

Based on this discussion, geographical range appears to support explanatory autonomy without depending on the problematic metaphysical claims that Kim has criticized. The emergent property is realized by a set of lower-level entities and properties, organized in the right way and arising from a complex sequence of lower-level causal interactions. How could such a property have distinctive causal powers? In a sense, it cannot. A species with a large geographical range cannot have any causal powers over and above the set of conspecific populations (organized just as they are). If so, then are not generalizations about range reducible to generalizations about organisms or populations? The answer is that although range size is determined by lower-level causes, insofar as geographical range size is both incompressible and causally salient, generalizations about range will be explanatorily autonomous. If range *per se* is causally salient, it is not the particular history nor the particular lower-level realization of range that is significant. Rather, it is range size. To capture the causal fact that range influences extinction risk, we need to appeal directly to this higher-level property because there is no 'short cut' or lower-level proxy for range as a causal factor. Thus, while any given *instance* of range size cannot have any causal power over and above its lower-level realization, there are causal facts about the

world (e.g. the relationship between range size and extinction) that cannot be captured by microevolutionary theory. It is a mistake to characterize this as merely epistemological emergence, as Silberstein and McGeever (1999) did. The explanatory autonomy reflects an ontological fact about the way the world of causes is structured.

The metaphysical account offered here fits nicely with the view that palaeontology and macroevolution, though irreducible, can be *locally* integrated with microevolutionary theory (Grantham 2004). Although some aspects of macroevolution and palaeobiology are irreducible, it will often be scientifically fruitful to co-ordinate micro- and macroevolutionary (or palaeontological and neontological) theories when they share common interests. For example, an inter-level theory could be developed which identifies the lower-level causes that determine geographical range and traces out their macroevolutionary consequences.

CONCLUSIONS

Several different theories of emergence are found in the philosophical literature: nominal emergence, non-aggregativity, weak emergence and strong emergence. These various accounts of emergence have a different bearing on the debate over macroevolution. In particular, nominal emergence and non-aggregativity are compatible with the explanatory reduction of macroevolution (i.e. the claim that the macroevolutionary domain can be explained by appeal to microevolutionary processes), while weak and strong emergence are more robustly non-reductionistic.

Geographical range appears to be emergent in a way that blocks the attempt to reduce macroevolution, even if no species selection on range occurs. According to Bedau's theory of weak emergence, geographical range is emergent if and only if four conditions are met: range (1) globally supervenes on lower-level properties, (2) results dynamically from the causal interaction of lower-level entities and properties in a way that is causally incompressible, (3) is crucial to the statement of higher-level causal generalizations or explanatory models, and (4) is nominally emergent at the species level. A review of the literature on range size suggests that geographical range meets conditions 1–3, though it may emerge nominally at the population level. Range supervenes on the spatial location of organisms and is, to the best of our knowledge, causally determined by a complex set of organismic- and population-level interactions. Crucially, however, these interactions are often non-linear and context-sensitive so that there is no 'short cut' for predicting range short of simulating the entire process. Although range is determined by a complex suite of lower-level processes, there are significant causal generalizations about range (such as its influence on extinction probabil-

ity and longevity). Together, these considerations suggest that range is weakly emergent and blocks reduction. Furthermore, it is likely that other lineage- and community-level emergent traits (such as evolvability and trophic structure) are also weakly emergent. If this analysis is correct, then macroevolution is not reducible to microevolution: adequate models of the macroevolutionary processes must make direct reference to emergent species-level properties.

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