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30 Years of Macroecology

The what, how and why of doing macroecology

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Abstract

Macroecology is a growing and important subdiscipline of ecology, but it is becoming increasingly diffuse, without an organizing principle that is widely agreed upon. I highlight two main current views of macroecology: as the study of large-scale systems and as the study of emergent systems. I trace the history of both these views through the writings of the founders of macroecology. I also highlight the transmutation principle that identifies serious limitations to the study of large-scale systems with reductionist approaches. And I suggest that much of the underlying goal of macroecology is the pursuit of general principles and the escape from contingency. I highlight that there are many intertwined aspects of macroecology, with a number of resulting implications. I propose that returning to a focus on studying assemblages of a large number of particles is a helpful view. I propose defining macroecology as "the study at the aggregate level of aggregate ecological entities made up of large numbers of particles for the purposes of pursuing generality".

KEYWORDS
macroecology, macroevolution, multicausality, philosophy of science, reductionism, transmutation problem

1 | INTRODUCTION

Macroecology is one of the major subdisciplines of ecology and is a rapidly growing field (Smith, Lyons, Morgan Ernest, & Brown, 2008). Although there was macroecological work done in the earliest days of ecology (von Humboldt, 1852), the field was named and defined as a distinct approach in 1989 (Brown & Maurer, 1989). Ironically, despite having a formal launch point (Brown & Maurer, 1989) and several textbooks (Brown, 1995; Gaston & Blackburn, 2000; Maurer, 1999), it is my sense that there is a lack of consensus about what macroecology is. At the British Ecological Society Macroecology meetings, it has become a standard practice (and a running joke) to ban discussions from the podium about how to define macroecology. And recently, when I told somebody I was writing a new macroecology textbook, their first question was whether it was the European or American flavour of macroecology. If there are distinct views on what macroecology is and how and why we should perform macroecology, we do not have to decide which one is right, but it is important for the field at least to know what the possible views (hence, sources of misunderstanding) are. This essay is my attempt to clarify two competing world views of macroecology, to trace their history and motivations and to trace some of the implications of adopting these views. I end by suggesting a more unified view of macroecology.

2 | VIEW 1: MACROECOLOGY = THE ECOLOGY OF LARGE SCALES

"Macro" comes from the Greek word μακρός, meaning long (or large). It is an obvious conclusion to assume that macroecology deals with large scales or systems. Indeed, in recent years I think it is fair to say that macroecology has become synonymous with large-scale ecology. This journal [*Global Ecology and Biogeography: A Journal of Macroecology* (GEB)] says in the first sentence of its scope statement that it "welcomes papers that investigate broad-scale (in space, time and/or taxonomy) ... patterns" and has used some variant of that for much of its existence.

Although the notion of what is large-scale ecology seems uncontroversial, and few have spent much time debating or seeking to define it, there are some interesting questions. First, as the GEB definition suggests, there are at least three dimensions to be large on: space, time and taxonomy (Figure 1). Early macroecology (Brown, 1995; Brown & Maurer, 1987; Maurer & Brown, 1988) focused on large in space and large in taxa ["studying … the assembly of continental biotas, specifically North American birds and mammals" (Brown & Maurer, 1989)]. The inclusion of time as a valid dimension to be large on has been a later emerging (and probably still developing) aspect of macroecology (although fully embraced by this journal). Among other things, this implies that macroecology embraces and overlaps with macroevolution and palaeoecology, something which I would heartily support.

Does macroecology require being large in all three dimensions (large time, space and many taxa; Figure 1)? I suggest that both by tradition and by practicality, macroecology does not require to be big simultaneously in all dimensions. For example, species abundance distributions have long been seen as macroecological (Brown, 1995; Gaston & Blackburn, 2000), but they often represent a single point in time and a small quadrat in space and thus are big only in the dimension of taxonomy. Conversely, there are extremely few examples of studies that are big in all three dimensions simultaneously. Some continental-scale palaeoecology papers (e.g., Lyons, 2003; Williams, Shuman, Webb, Bartlein, & Leduc, 2004) might be the only examples I know. I would therefore argue that big in one dimension is enough. The current Editor-in-Chief team at GEB also applies this definition of being big in one dimension as suitable in scope for GEB.

More fundamentally, I am not aware that anybody has put a more formal definition of how to define large (i.e., macro) in the literature beyond the aforementioned quote from Brown and Maurer (1989) about continental and "birds or mammals". It seems obvious that large needs to be defined relative to the organisms involved. Macroecology of bacteria could conceivably occur in a large Petri dish over a week, whereas macroecology of trees will require subcontinents and millennia. I suggest defining macro by the notion of dozens. Large time covers dozens of generations (long enough for evolution and changes in community composition to occur). And large taxa would cover dozens of species (enough for macroevolution to occur). Large space contains dozens of populations of a species. The size of a population is not itself well specified, but here I take a population to be big enough to have most of the dynamics occur endogenously to that population and be unlikely to go extinct stochastically. Thus, each population has presumably hundreds if not thousands of individuals. For typical macro-organisms, such as vertebrates and seed plants, and admittedly being very arbitrary, large might mean at least decades to centuries, all species in a taxonomic order or class, and subcontinental (i.e., a non-trivial fraction of a continent or, if you prefer, at least a good-sized country or large island archipelago). These definitions imply that < 5% of ecological studies are large in either space or time (Estes et al., 2018).

Finally, anybody who has studied the theory of scale knows that scale has both grain and extent. These have often been seen as correlated (large extent implies large grain size); therefore, the distinction was unimportant in defining large-scale studies. Indeed, historically that has been true. Continental-scale datasets typically had a coarse grain, whether it was a 25-mile breeding bird survey route (Robbins, Bystrak, & Geissler, 1986; Sauer, Hines, Gough, Thomas, & Peterjohn, 1997) or a state- or county-level checklist or a 10 km × 10 km grid grid. But it is possible, and increasingly common, to have a large extent and a small grain size. Driven in large part by interest in climate change, we are seeing many studies that cover thousands of kilometres, if not the whole globe, in extent, yet have a grain size of a few square metres or less. One of the better-known examples is the NutNet (Nutrient Network) collaboration (Borer et al., 2014), with global extent but plots of 25 m^2. This journal also sees many submissions that cover most or all of the geographical range of a species but deal with the population parameters of small, local populations of a single species. I think the jury is still out on whether such large-extent, small-grained data will turn out to be considered macroecological (albeit they are obviously good science whatever you call them). It is also worth noting that although there are few trends in the scales we study (i.e., most of ecology is still just as small scale as it was several decades ago), extents are becoming larger, whereas grain size is unchanged (Estes et al., 2018). This question of what to make of large-extent, small-grained studies is therefore only becoming more frequent.

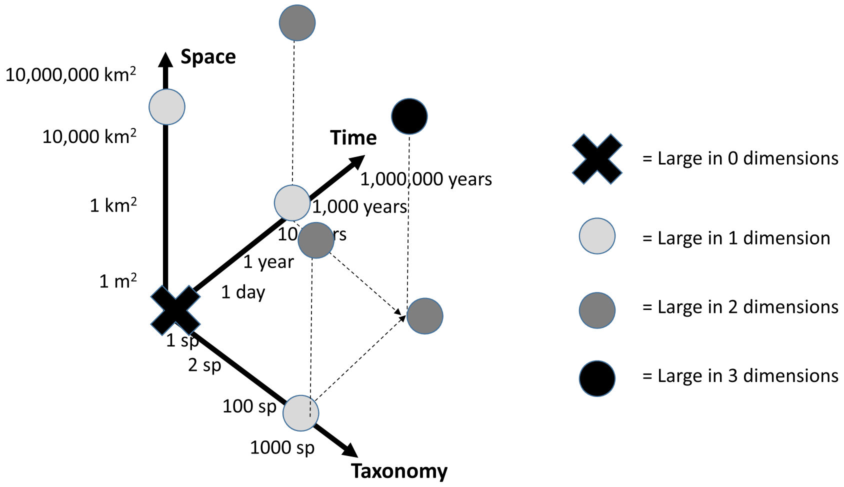

FIGURE 1 How many dimensions does it take to be large scale? Space, time and taxonomy are three dimensions of every ecological (biological?) system. A system can be relatively large or small in each of these dimensions. To qualify as large scale, how many dimensions must be large? [Colour figure can be viewed at wileyonlinelibrary.com]

Details of definition aside, there are plenty of reasons to embrace the notion of macroecology as equivalent to studying large scales. Simply advocating for studying large scales is novel and important in itself. The vast majority of ecology is done on spatial scales that would fit on a tabletop or within a room and within a timespan of a single grant or thesis (Estes et al., 2018; Maurer, 1999; Smith et al., 2008); therefore, studying large-scale ecology is in itself radical. The motives for studying large scales are many. Personal preference is one. As somebody who is fascinated by climatology, geography and palaeontology, it is not surprising that I prefer large-scale ecology, just as it is not surprising that somebody who loves handling a rodent might prefer micro-scales. There are also obvious conservation and applied motives for studying large scales. Whereas a classic endangered species-focused conservation approach favours understanding the physiology, behaviour and population dynamics of a species (i.e., small scales), the increasing focus on biodiversity and global change in conservation favours studying large scales, as do the primary regulatory and decision-making frameworks of modern society that place decisions in the hands of land managers, who usually manage land on the scales of square kilometres.

3 | THE HISTORY OF THE MACROECOLOGY = LARGE-SCALE ECOLOGY VIEW

Ironically, despite the etymology of the name macroecology, many of the earliest practitioners of the field do not seem to have seen size as the central feature or even to have seen macroecology as exclusively about large scales. For example, Brown and Maurer (1989) list five key features of macroecology, none of which is spatial scale. And they suggest that "[Macroecological] analyses also provide evidence of the processes that couple ecological phenomena that occur on disparate spatial and temporal scales—from the activities of individual organisms within local populations to the dynamics of continent-wide speciation, colonization, and extinction". Lawton (1999) said, "Macroecology is the search for major, statistical patterns in the types, distributions, abundances, and richness of species, from local to global scales." Most explicitly, Brown (1995) said, "[Macroecology] is a non-experimental, statistical investigation of the relationships between the dynamics and interactions of species populations that have traditionally been studied on small scales by ecologists and the processes of speciation, extinction, and expansion and contraction of ranges that have been investigated on much larger scales by biogeographers, palaeontologists and macroevolutionists." Gaston and Blackburn (2000) open their book with a discussion of patterns found in birds on a single day in Wytham Woods (a relatively small patch of land and a short time period relative to the lifespan of a bird) and then note how the patterns observed then/there link to much larger patterns of the avifauna of Britain. These authors clearly saw macroecology as including local scales even while making explicit the need to place local systems in a large-scale context. Macroecology was more an intentional unification of small and large scales, not solely about large scales. It was just that studying small scales was already extremely common (Estes et al., 2018; Gaston & Blackburn, 1999; Maurer, 1999; Smith et al., 2008), whereas studying large scales was the novel (but not exclusive or central) contribution of macroecology. But studying large scales did not seem to be the definitional feature of macroecology in most cases.

It was only a little bit later in the development of the field that its proponents began to home in on size and scale as its central feature [e.g., "The field of macroecology is concerned with understanding the division of food and space among species at large spatial (geographic) and temporal scales" (Gaston & Blackburn, 1999)] or still more focused on size ["Macroecology is concerned with understanding the abundance and distribution of species at large spatial and temporal scales" (Gaston & Blackburn, 2000)]. Thus, the view that macroecology was primarily defined by its study of large scales appeared only partway into the development of the field, although it is likely to be the predominant view today.

4 | VIEW 2: MACROECOLOGY = TAKING A STATISTICAL, EMERGENT, NON-REDUCTIONIST APPROACH

If some of the original authors, such as Brown, Maurer and Lawton, saw macroecology as spanning across small and large scales, what was their view of what was the essential defining feature, the *sine qua non*, of macroecology? A good example of this second view is (Smith et al., 2008):

> Macroecology is a big-picture, statistical approach to the study of ecology. By focusing on broadly occurring patterns and processes operating at large spatial and temporal scales and ignoring localized and fine-scaled details, macroecology aims to uncover general mechanisms operating at organism, population and ecosystem levels of organization.

It may be easier to describe what this second approach is not (reductionist) than what it is. Reductionism is the view that the way to understand a system is to break it up into component parts and study the behaviour of the parts in isolation and then their interactions with each other. The reductionist view is prevalent in ecology. And the reductionist view was specifically central throughout the 1970s–1990s to community ecology in its attempt to explain community-level patterns by studying pairwise interactions of species. People are now advocating that a reductionist view is crucial to advancing macroecology (Connolly, Keith, Colwell, & Rahbek, 2017).

In contrast, several of the early proponents of macroecology were heavily influenced by the field of complex systems (Brown, 1994; Kauffman, 1993; Maurer, 1999). Words such as statistical, holistic, phenomenological and emergent have been used to describe the best way to study complex systems. For example (Gaston &

Blackburn, 1999), “complex systems frequently exhibit properties or behaviors that arise from the interaction of their constituent parts. These emergent properties may have been predictable with hindsight (although perhaps with difficulty, or as one of several possible outcomes), or may have been completely unpredictable given knowledge attained from the study of the constituent parts of the system.” Maurer (1999) specifically invites an analogy to statistical mechanics in physics: “matter is ultimately made up of a large number of small particles with stochastic properties. Thus, in [Schrodinger’s] view, regular, repeatable laws of classical physics were only approximations. … there are so many small particles involved in phenomena like gravitation, magnetism, and diffusion, that the uncertainty they encompass becomes insignificant. The law of large numbers hides, so to speak, the uncertainty of these physical processes from us.” Thus, even though the movement of individual microparticles or gas molecules may be random, their collective behaviour is highly predictable at an aggregate level. Gaston and Blackburn (2000) talk about the bottom-up (reductionist) and top-down (emergent) approaches.

The contrast between reductionism and emergentism is not unique to ecology (although reductionism is especially strong in ecology). John Maynard Smith, one of the giants of evolution and evolutionary ecology, describes this split as a very general phenomenon of science and suggests that individual minds are pre-adapted to one view or the other. Maynard Smith (1997) said:

> There are two kinds of mathematical or formal theory that one can make in science. One is a sort of microscopic theory. You try to explain the behavior of something in terms of its components and the way they interact and so on. And there are what one might call phenomenological theories, which describe the behavior of systems in terms of measures made on whole things….
>
> It seems to me that most scientists think in one of those modes but not both. I think if you’re a genius, you might be able to think in both, but most of us either think in microscopic models or global, descriptive sorts of models. I am a microscopic man. I cannot think—I never understood entropy, even when I was an engineer. I could look it up in the tables but it never meant anything to me at all. I’m a microscopic man….
>
> But it is very striking that there isn’t just one way of modelling the world. There are often two ways of modelling the same phenomenon and depending on what kind of mind you have, you may find one way or the other illuminating.

Maynard Smith is sincere that both approaches are equally valid and simply a function of how one’s mind works, not that one way is better or more right, even as Maynard Smith is very clear that he himself prefers the micro way.

5 | THE TRANSMUTATION PROBLEM NECESSITATES A DISTINCT MACRO APPROACH

A common response to the choice to focus on an emergent or macro approach is that you do not have to choose. If you are interested in macro-phenomena, simply explain them by scaling up the micro-phenomena. This sometimes veers into fairly value-laden judgements that the “best way” to do science is reductionism. Of course, this suggestion is simply a restatement of the reductionist view and, as such, is a rather circular argument for the superiority of the reductionist approach. It notably fails to embrace Maynard Smith’s view that both approaches are valid and that preference is an individual choice.

Salt (1979) defines “‘An emergent property of an ecological unit is one which is wholly unpredictable from observation of the components of that unit.’ The corollary is: ‘An emergent property of an ecological unit is only discernable by observation of that unit itself’.” The reductionist view rejects the possibility that there can be such a thing as an emergent property by Salt’s definition. In the reductionist view, adequate modelling of the components should always reproduce all emergent phenomena.

Importantly, it can be shown mathematically that even in relatively simple conditions the reductionist programme of scaling from the micro to the macro can be very hard and necessarily involves the loss of accuracy. This point was first made by O’Neill, in what he called the “transmutation problem” (O’Neill, 1979). O’Neill shows how the simple mathematical process of scaling up transmutes (changes) step functions into linear functions and moves the locations of peaks or optima, among other examples. This is one of the more profound yet almost completely unknown papers in ecology, in my opinion, leading to multiple reinventions of the same idea (Chesson, 1998; Englund & Cooper, 2003; Rastetter et al., 1992).

The mathematical details of the transmutation problem are given in Box 1. A brief summary is that scaling up is challenging because of Jensen’s inequality, which states that the average of a function is not the function of the average (Figure 2). Jensen’s inequality highlights the two factors that make scaling in ecology hard: nonlinearity and variance. This means that mean-field models are at best approximations, which become progressively worse as a system has more nonlinearity and variance. This suggests that, short of measuring every location on the globe (which is done for weather forecasting), using an emergent model at the level of objects and properties of interest is likely to be more productive and accurate than building a reductionist model based on components.

A concrete example of how micro-scale processes fail to scale to the macro-level is the following. In a study of productivity versus rainfall (Huxman et al., 2004; Figure 3), the relationship between rainfall and productivity within a site across years is found to be approximately linear, with highly variable slopes and intercepts, whereas across a continental gradient the relationship (Figure 3) is found to be a saturating function (similar to the curve shown in Figure 2). Within sites, the key mechanism is the water use efficiency (WUE) of the community driven

BOX 1. MATHEMATICAL DESCRIPTION OF THE TRANSMUTATION PROBLEM

Imagine two scales, the micro-scale and the macro-scale. For example, the individual 1 m × 1 m quadrat plot might be the micro-scale, and a 10 km × 10 km park might be the macro-scale. Imagine there is an independent variable of interest, x_i (perhaps rainfall), and a dependent variable of interest, y_i (perhaps plant productivity), at the micro-scale, where i indexes the 100,000,000 distinct quadrats. One can (and ecologists have) develop detailed models for the relationship between rainfall and productivity (e.g., Huxman et al., 2004). Denote this model by the function, f, and a parameter, θ, representing soil, topography, species composition or other local conditions that varies by quadrat: i.e., $y_i = f(x_i, \theta_i)$. But somebody interested in the macro-scale (i.e., our 10 km × 10 km park) for whatever reason will want to know the behaviour of the variable at a much larger scale (macro-scale). Denote the two variables measured at the macro-scale by X and Y (park-wide rainfall and park-wide productivity in our example) with an emergent, macro-scale modelling, linking them, of $Y = F(X, \Theta)$. Can we use our micro-scale model f to tell us anything about the macro-scale model F? This, in its essence, is the claim that we do not need emergent approaches because everything can be built up from reductionist approaches. In most cases, we can relate X to x_i by either $X = \Sigma_i x_i$ or $X = \overline{x_i}$. The first group is what statistical mechanics calls extensive variables (they are summed across systems). Extensive variables in ecology include variables such as the abundance of a species or total community productivity. The second group that uses an average [which might need to be a weighted average if the sizes of the micro-units (e.g., quadrats) vary in size] is called intensive variables. In ecology, they include such things as population density, temperature, occupancy or productivity per unit area. Of course, ecology has some variables, such as species richness, which are neither intensive nor extensive (because they are neither constant nor linear functions of area), in which case even a relationship between x_i and X is not possible.

Moving to understanding the macro-variable Y and model F, if we assume that Y is an intensive or extensive variable, then an obvious approach is simply to model each quadrat and aggregate up the results; that is, to study $Y = \Sigma_i y_i = \Sigma_i f(x_t, \theta_i)$ or $Y = \overline{f(x_i, \theta_i)}$ depending on whether Y is extensive or intensive, respectively (recall that a bar over something implies taking an average of that something). This is mathematically correct. However, this approach requires considerable resources to obtain x_i and θ_i for every single quadrat and considerable computational resources to calculate a complex nonlinear model for every quadrat. I call this the weather approach to scaling because it is the route we have taken for weather forecasting, where we spend billions of dollars annually to measuring conditions precisely all over the world and run global circulation models (GCMs) on supercomputers to forecast the weather. Despite this investment and the fact that the physical principles of atmospheric dynamics (i.e., nature of f) are fully known, we have accuracy only 3–5 days into the future. This is a tangible example of the difficulty of scaling up.

Given the practical costs of the weather approach, it is very tempting to take the detailed process-based model and study it on an "average" quadrat [i.e., $f(\overline{x_i}, \overline{\theta_i})$], because such data are often available, and this model is computationally tractable, hence much more feasible to study. This is known in physics as the mean-field approach to scaling and is a common modelling tactic. Many assume this will give the correct answer for the coarse scale problem (X) by summing up [i.e., $Y = n\,f(\overline{x_i}, \overline{\theta_i})$ (where n is the number of quadrats)]. However, it requires that $nf\left(\overline{x_i}, \overline{\theta_i}\right) = \sum_i f\left(x_i, \theta_i\right)$ or, equivalently, that $f\left(\overline{x_i}, \overline{\theta_i}\right) = \frac{1}{n}\sum_i f\left(x_{i,t}, \theta_{i,t}\right) = \overline{f(x_i, \theta_i)}$. Unfortunately, it is well known from Jensen's inequality (Jensen, 1906) that, in general, it is not true that $\overline{f(x_i)} = f(\overline{x_i})$. The equality holds if and only if either $f(x)$ is a linear function or the variance of $x_i = 0$. Thus, the mean-field fails when both f is nonlinear and when there is variance in x_i. And the failure can be large, not merely a mathematical detail. Errors of the magnitude of 10% are typical [Figure 2; examples in the paper by O'Neill (1979)]. Of course, the likelihood both that f is nonlinear and that there is variability in the x_i (and/or the θ_i) is very high in ecology. We can approximate the error using Taylor's series and including a second-order term: $\overline{f(x_i)} \approx f\left(\overline{x_i}\right) + f''\left(\overline{x_i}\right) \mathrm{var}(x_i)/2$ (where f'' is the second derivative of f; i.e., a measure of its nonlinearity). The Taylor expansion can also be extended to θ. This gives a clear indication of the sources of error and shows that the error increases as the product of the degree of nonlinearity (f'') and variability [$\mathrm{var}(x_i)$].

An alternative approach is to build a macro-level model approach to scaling: $Y = F(X, \Theta)$. Here, Θ is a vector of the parameters at the macro-level. This is the emergent approach of studying the system properties at that level. We have shown that F is likely not to be the same as f (or even derivable from f). This translates ecologically to the fact that because we have changed scales, F could be based on completely different processes from f. Figure 3 gives a real-world example.

It gets worse. So far, I have examined only static scenarios. Now, imagine that we are looking at a differential or difference equation, so we have $x_{i,t+1} = g(x_{i,t}, \theta_i)$, and g is chaotic. Then, by the definition of chaos, small initial errors are magnified exponentially fast. In the weather scaling scenario, the loss of forward predictability is attributable only to errors in the measurement of $x_{i,t}$ and θ_i. But in a mean-field or delta-rule scaling scenario, errors attributable to Jensen's inequality are also introduced. In practice, this means there is no predictive relationship possible more than a few time steps forward. Thus, the possibility of scaling temporal difference/differential equation models is very dim. Englund and Cooper (2003) review a number of other reasons why processes in small patches might change in importance in large patches. Most importantly, the perimeter-to-area ratio changes with scale, which means that the importance of internal dynamics versus boundary dynamics (i.e., immigration and emigration) changes with scale.

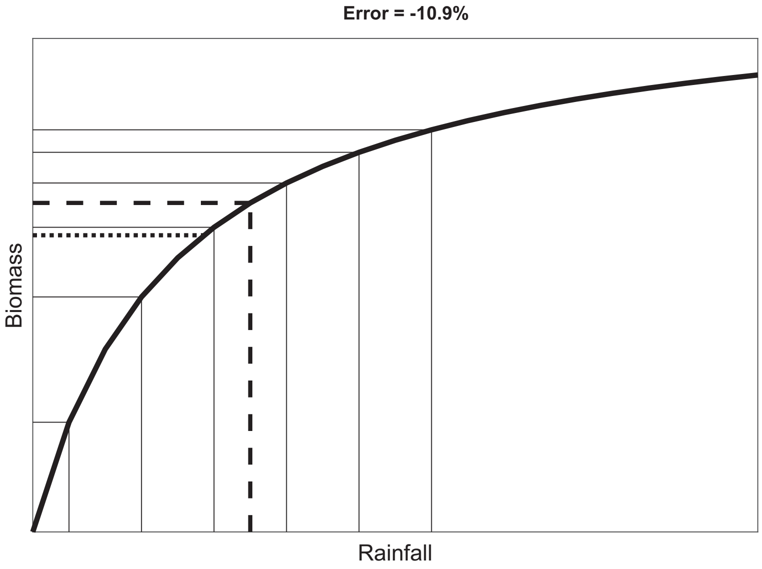

FIGURE 2 An example of Jensen's inequality. When there is a nonlinear relationship between two variables (continuous thick curved line) and variation in the *x* values (here, six distinct x_i values are shown by the vertical thin lines), then $\overline{f(x_i)} \neq f(\overline{x_i})$. Each of the $f(x_i)$ are shown by the horizontal thin lines. Here, $\overline{x_i}$ is shown by the thick dashed vertical line, and $f(\overline{x_i})$ is shown by the thick dashed horizontal line connected to it. In contrast, $\overline{f(x_i)}$ is shown by the isolated thick dotted horizontal line (and is the average of the six thin horizontal lines). The distance between the thick dashed and the dotted horizontal lines is the error of the mean-field approximation. In the example in this figure, the error of approximating $\overline{f(x_i)}$ by $f(\overline{x_i})$ is 10.9%. Nothing about this example is atypical of ecology

by the physiological plasticity of individual plants to water availability. For example, in water-limited sites, stomata were probably opened more in wet years, allowing more photosynthesis to occur. But across sites, the key factor is the varying composition of species present at different locations across North America. The different species are sampled from different ends of the water-conserving versus fast-growing trade-off (Figure 3). It is important to note that in this example both the patterns (straight line versus saturating curve) and the processes (physiology versus species composition) changed between the micro-scale and the macro-scale.

In truth, even in physics the ability to scale is much more limited than people realize. The examples of scaling from the velocities of molecules to emergent properties of diffusion rates in Brownian motion diffusion theory or to temperature and pressure in statistical mechanics are cited so often because they are about the only successful applications of scaling in physics. Gravity has never been reduced to explanation by its component parts (gluons have been hypothesized but have received no empirical support). And chemical engineering principles are not reducible to quantum mechanics or statistical mechanics owing primarily to the spatially and temporally heterogeneous and turbulent nature of a real-world chemical vat.

As a matter of practicality, it can be very hard to take important ecological factors and identify any sense in which they are a component. Ambient temperature and its influence on an individual organism provide an example; ambient temperature can be very important in the behaviour and physiology of a lizard, but in what sense is temperature a component part? What limits would you have to put on a system to make ambient temperature a component? And are you studying a different system by the time temperature becomes only a component? Is it not much cleaner to examine the context in which objects of interest are embedded, instead of merely insisting that we have to break the object of interest (the lizard) into components to do good science (McGill & Potochnik, 2018)?

Thus, the claim that macroecology can be explained by individuals and population dynamics can be demonstrated rigorously to be possible only rarely, owing to the transmutation problem (Box 1). Necessary conditions to scale from the reductionist approach

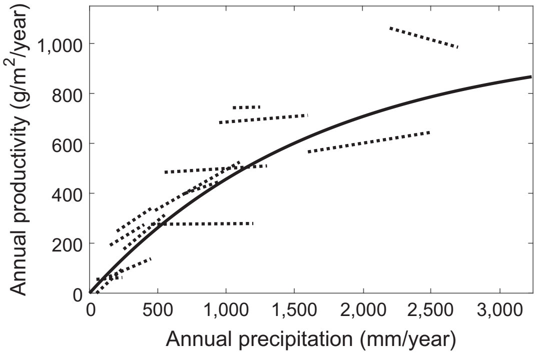

FIGURE 3 Micro- and macro-scale relationships between rainfall and productivity. Dotted lines indicate between-year variation in productivity and rainfall at a single site. The continuous curved line indicates the overall across-site trend. Within-site variation is attributable to physiological responses of plants growing at that site to temporal variation in rainfall. Between-site variation is attributable to changes in species composition along a spatial rainfall gradient. Redrawn from Huxman et al. (2004)

include variables that are purely intensive or extensive (e.g., not species diversity), lack of variability across reductionist components, linearity in relationships between variables, and equilibrial (non-chaotic) models. If there is one thing the last 100 years of ecology have taught, it is that most often ecology is the opposite of this. Therefore, understanding emergent properties is going to happen only by studying and building models at the emergent, systems level, not by a reductionist approach. This is not to deny that there is some philosophical sense in which causality flows from small parts to large. It is simply that this tautological flow of causality is of little practical or predictive use in studying the whole system and its emergent properties. The physicist turned ecologist, MacArthur (1972), clearly stated this decades ago: "(m)ost scientists believe that the properties of the whole are a consequence of the behaviour and interactions of the components. This is not to say that the way to understand the whole is always to begin with the parts. We may reveal patterns in the whole that are not evident at all in its separate parts."

6 | ONE MOTIVE FOR AN EMERGENT APPROACH ARISES FROM A MULTICAUSAL, CONTINGENT WORLD

The transmutation problem suggests that an emergent, non-reductionist approach is needed if one wants to study large scales, which some scientists will be motivated to do. But I suggested that many early macroecologists started not from an insistence on large scales, but rather with an insistence on emergent/non-reductionist approaches. What directly motivates an emergent/non-reductionist approach?

I would suggest that it is the pursuit of generality. And I would argue that the push for generality (which in turn drives the push for emergence) is rooted in the increasingly apparent limitations of the approach of small-scale experiments, which were dominant in the 1990s when macroecology was launched as a field. The initial paper by Brown and Maurer (1989) defining macroecology notes about experiments: "The problem, however, is not so much in interpreting the outcome of any single experiment as in synthesizing the results of many different studies to draw useful generalizations about the organization of the world." The book on macroecology by Brown (1995) opens with the contrast of a population-level experimental approach (which he calls "traditional microscopic") and a macroecological approach to answer a specific question about climate change and species ranges in mountains. Brown is clear that he himself is a frequent practitioner (and appreciates the power) of the traditional microscopic approach. But he then goes on to note that in terms of providing a general answer, "The results [of a microscopic approach] while valuable would be limited. There would never be enough time and money to study all species populations on all mountaintops. A great deal of questionable extrapolation to other populations of the same species on other mountain ranges and to different, unstudied species on the same mountain ranges would be required."

Lawton (1999) is even more explicit. Lawton poses the question of when one can expect ecology to produce general laws. He notes that population dynamics deals with very simple systems (one species, one or a few causal factors) and thus finds population dynamics to be tractable and able to produce general laws. He then tackles community ecology, where he spent much of his career. His summary is that:

> Although we now have a good understanding of how several local sets of interacting species work in nature, the problem is that we have no means of predicting which processes will be important in which types of system. To that extent, work on communities is no different to work on population dynamics. The difference is in the mind-boggling degree of contingency involved in work on communities.

The fact that several people who had a spent a significant fraction of their career exploring a reductionist experimental approach to community ecology came to this conclusion almost simultaneously in the 1990s probably represents a communal frustration. The small-scale experimental approach of the 1970s–1990s came into existence in no small part as a backlash to a simplistic model approach in the 1960s and 1970s (Resetarits & Bernardo, 1998). In turn, macroecology arguably emerged in no small part as a response to the frustrations and limitations of the small-scale experimental approach. It might even be fair to suggest that 20–30 years later, macroecology is experiencing its own backlash, with people wanting to make macroecology more reductionist (Connolly et al., 2017) and experimental (e.g., the topic of a symposium on "Experimental Macroecology" at the International Biogeography Society meeting in Tucson in 2017). Thus, the cycle of frustration may be closing 40–50 years later.

But to return to the communal frustration with small-scale experiments of the 1990s, and Lawton's expression of it, Lawton (speaking from his decades of personal experience) believes that no general laws can emerge in community ecology. There are many possible forces acting on a community, and which one is most important will change over time and across locations (not to mention from species to species). Lawton's summary of his decades of work in community ecology is a subsection with the heading, "Too much contingency". The closely interrelated ideas of many causal factors (which I will call multicausality) and contingency can be expressed by Figure 4. Imagine a focal species of mouse (centre of Figure 4). Now start listing the things that could affect the abundance of this species. Predation, resources such as plants producing seeds, temperature and disease are all possible. Other predators (e.g., raptors), different diseases, other resources, habitat (for predator safety and thermal regulation), other climate factors and anthropogenic factors (e.g., land use change) can all be invoked. It is no exaggeration to say that dozens of factors can influence our target species of mouse. Which is most important? Well, many of these factors have been documented in studies where the target factor was presumably an important if not the most important, factor. This is where the problem of contingency comes in. Is it a cold year (or a northern

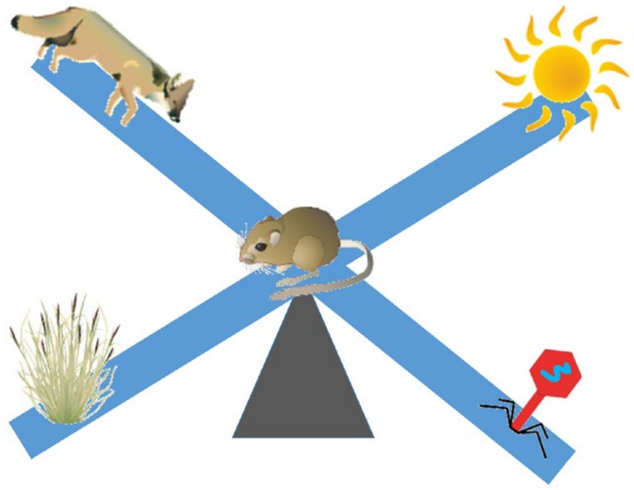

FIGURE 4 The multicausal, highly contingent nature of ecology. The target species (a mouse) is influenced by many factors, ranging from predators (e.g., a fox) to resources (e.g., grass seeds) to climate to diseases. At a given moment, any of these factors can be in ascendancy, and relatively little change is required to tip to another factor being dominant. Mouse, fox, sun, grass and virus drawings courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/) [Colour figure can be viewed at wileyonlinelibrary.com]

location)? Then temperature is probably among the most important factors. Is it a dry year (or location)? Then rainfall and seed productivity are probably important, etc. The problem is that these factors are close enough to each other in importance that any of them can swing into ascendency as the most important at some times and in some places. A morass of contingency emerges from the many, many possible factors, as suggested by the four-way seesaw in Figure 4. At any given time or any given location (Figure 5; also see Wimberly, Yabsley, Baer, Dugan, & Davidson, 2008), any one of the factors can be elevated.

The fact that community ecology has dozens of potentially important forces, leading to a high degree of contingency, is a frequent observation in ecology. Many approaches seek to embrace and harness this contingency. MacArthur (1972) suggests "[one should erect a] two- or three-way classification of organisms and their geometrical and temporal environments, this classification consuming most of the creative energy of ecologists. The future principles of the ecology of coexistence will then be of the form 'for organisms of type A, in environments of structure B, such and such relations will hold'."Schoener (1986) goes even further and proposes an 18-dimensional classification of ecological systems!

Like the approaches of MacArthur and Schoener, a macroecological approach identifies the reality and challenge of multicausal contingency of ecology. But instead of embracing and stepping

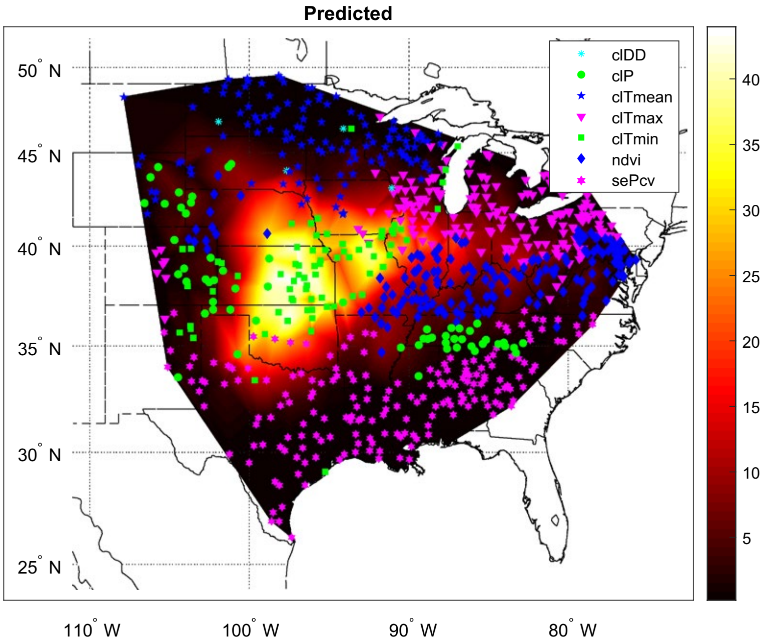

FIGURE 5 Different climatic factors limit the population size of the scissor-tailed flycatcher at different locations in its range (B. McGill, unpublished observations). Data from North American Breeding Bird Survey (Patuxent Wildlife Research Center, 2001; Robbins et al., 1986; Sauer et al., 1997). At some northern sites, temperature [either total summer warmth measured by degree days (clDD) or winter minimum temperature (clTmin)] is limiting. Other factors are limiting at other sites (clTmean is mean annual temperature, clTmin is minimum monthly mean temperature, clP is total annual precipitation, ndvi is a satellite measure of productivity, sePcv is a measure of precipitation seasonality based on the coefficient of variation across months, and seTsd is a measure of temperature seasonality based on a standard deviation of monthly temperatures). The limiting factor is identified by fitting Gaussian quantile curves to abundance versus a single environment variable. Whichever variable at a site predicts the lowest abundance is considered limiting [Colour figure can be viewed at wileyonlinelibrary.com]

into this reality by trying to classify our way through it (i.e., reducing the dimensionality from hundreds of dimensions to a handful of dimensions), macroecology seeks to side-step the whole problem. In statistical terms, MacArthur and Schoener wanted to do a dimension reduction like principal components analysis, whereas a macroecologist wants to use a central-limit theorem argument. As Lawton (1999) says, “Macroecology … seeks to get above the mind-boggling details of local community assembly to find a bigger picture, whereby a kind of statistical order emerges from the scrum.” Brown and Maurer (1989) and Maurer (1999) suggest a statistical mechanical approach as the path away from multicausal contingency. In this view, individuals or species become particles, and although the behaviour of one ecological particle is highly unpredictable (owing to multicausal contingency), the behaviour of the ensemble of many particles again becomes predictable (exactly as the behaviour of a gas ensemble of particles is predictable). Or as Brown (1995) notes:

> Macroecology is self-consciously expansive and synthetic. In this respect it does differ philosophically from much of traditional ecology, which I would characterize as becoming increasingly reductionist and specialized. Rather than trying to use ever more powerful microscopes to study the fine details of ecological phenomena, macroecology tries to develop more powerful macroscopes that will reveal emergent patterns and processes. To make an analogy, the goal is not to understand a tapestry in terms of warp and woof and the chemistry of fibers and dyes, but to see and interpret the entire scene. In order to visualize the big picture it is necessary to stand back and take a distant view. Accordingly, macroecology attempts to increase the spatial and temporal scale of ecological inquiry, and also to expand the kinds of questions asked and the range of phenomena studied.

Note how explicitly here the “increase [in] the spatial and temporal scale of ecological inquiry” is invoked not as an end in itself to study large scales, but rather as a means to the end of generality that escapes from multicausal contingency that is rampant in ecology. This is echoed in the definition of macroecology by Smith et al. (2008) quoted at the beginning of the Section 4 on view 2 of macroecology.

7 | THE INSISTENCE ON EMPIRICISM IN MACROECOLOGY: A COMMON THREAD TO BOTH DEFINITIONS

Although I have drawn a contrast between two visions of what it is to do macroecology, I believe there is one commonality that both views clearly share. This commonality is a very high degree of empiricism centred on observational and comparative approaches. The fact that macroecology rejected experimental approaches during its origins is pretty clear. Whether this is because of the impracticality of experiments at large scales (view 1) or because of the difficulties of producing generalities from experiments (view 2), one ends up in the same place. Although much less universal, Maurer (1999) carefully prosecutes a rejection of the models then in ascendency in the 1990s. By the 1990s, models had moved from simple (and empirically informative) Lotka–Volterra and Rosenzweig–MacArthur models of species interactions towards a community matrix approach that modelled many species and interactions simultaneously.

When one does not require experimental proof of mechanism, abandons reductionist norms of causality, embraces a statistical view and deals with emergent properties that cannot be traced to their component parts, the net effect appears to be a much greater embrace of correlation, regression and trendline statistical methods. Maurer (1999) is the only one explicitly to build a case for this, but it is universal in the methods used in early macroecology. Although not frequently described, macroecologists seem to place a high value on raw empiricism, the central importance of what the real world tells us. And this involves embracing data. Very large amounts of data if we want generality! This is not to say that macroecology is purely correlational or lacking in rigour; it is simply that the rigour has to come from careful thinking and careful application of tools such as null models and the comparative method (Blackburn, this issue; Gaston & Blackburn, 1999, 2000). It is not that macroecology rejects models. It does not (Brown, 1984; Harte, Zillio, Conlisk, & Smith, 2008; Marquet et al., 2014; Maurer & Taper, 2002). But models need to be in the service of explaining the general patterns found in the real world, not proliferating in complexity. It is a question of priorities; macroecology prefers general patterns repeatedly found in empirical data both over reductionist models unmappable to the real world and over claims of non-general causality from small-scale experiments.

8 | A LESSON FROM OTHER MACRO FIELDS: FOCUS ON LEVELS OF AGGREGATION AND NUMBER OF PARTICLES

This essay has addressed only macroecology. But at least two other fields explicitly recognize a macro/micro distinction. Macroevolution deals with evolution above the species level (Stanley, 1975), whereas microevolution deals with evolution within a single species (i.e., the modern evolutionary synthesis). The field of evolution also exhibits a strong push to insist that “macroevolution is just the cumulative effect of microevolutionary forces” (Hendry, 2018). But palaeontologists and phylogeneticists recognize emergent patterns, such as variation in speciation rates through time, that may reduce tautologically to microevolution but cannot, in any meaningful way, be studied or explained by microevolution. Likewise, economics is divided into microeconomics versus macroeconomics. Macroeconomics emerged in the 1930s from work of John Maynard Keynes as an attempt to understand the Great Depression. Macroeconomics deals with the economies of nations, whereas microeconomics deals with the decisions of households and companies. I would suggest that all three macro-fields share similarities. That is (echoing Maynard Smith) "going macro" is a general attack on understanding the world that is shared across ecology, evolution and economics. All three macro-fields are emergent, study larger scales and have problems with simplistic, differential equation, equilibrial models that are prevalent in the micro versions of their fields. All three fields turn instead to let-the-data-speak statistical models, such as correlations and trendlines.

I do think that identifying this commonality with other macro-fields points to a possible lesson that macroecology could learn from macroeconomics and macroevolution. In macroeconomics, the move was from studying households and companies to studying nations. Certainly, typical nations are spatially larger than companies or households. But the more relevant relationship is that a nation is made up of many, many households and companies, and by studying a national economy at the emergent level we can look at statistical averages across companies and households rather than needing to understand the details. And in macroevolution, the definition is very explicitly focused on moving from individuals within a species to comparison across species. Certainly, there is an accompanying expansion of temporal scales. But in both the macroeconomic and macroevolutionary cases, the key definitional aspect is a shift in organizational level (from a household/company to a nation; from individuals within a single species to many species). Perhaps macroecology should define its sense of increasing scale not in terms of spatial, temporal and taxonomic scales, as I and most macroecologists have done, but rather in terms of the units of study or levels of aggregation, as macroeconomics and macroevolution have done. How would it change macroecology to focus on sets of species (be they local communities or regional pools) as the primary meaning of going large (i.e., going macro)? I think the original founders of macroecology probably perceived scale in this fashion. Brown and Maurer (1989) emphasized the study of assemblages and the inclusion of the species abundance distribution of a single quadrat as a macroecological topic.

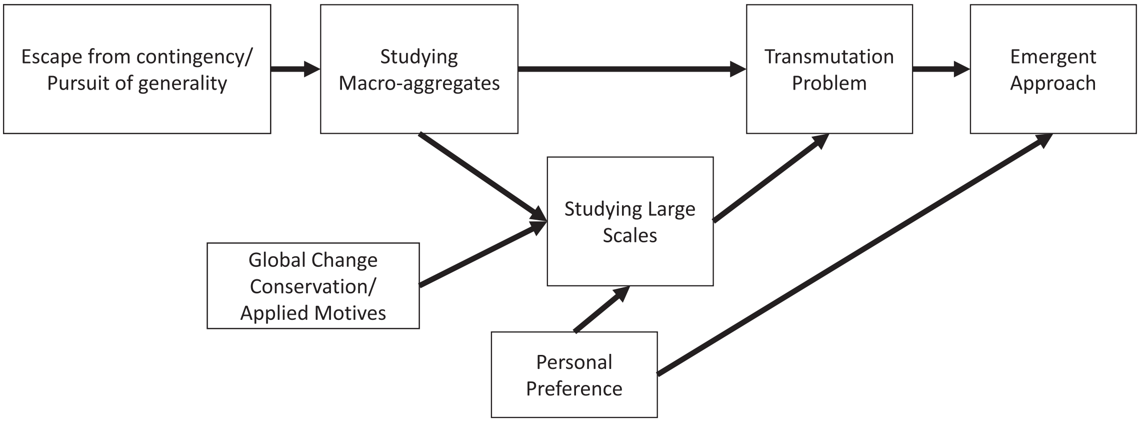

FIGURE 6 A summary of the motives, goals and approaches to macroecology and how they imply additional motives, goals or views

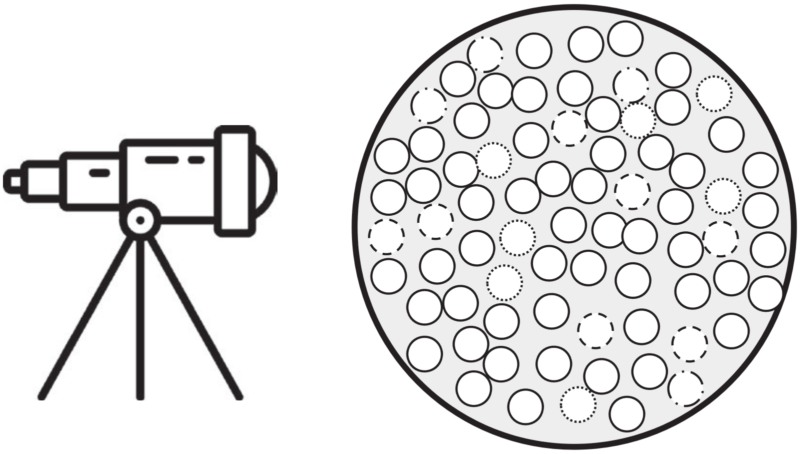

FIGURE 7 An illustration of my proposed definition of macroecology. The large grey circle is an aggregate entity. It is composed of many particles. The particles are similar and comparable but may show variation. Macroecology chooses to study (the telescope in this illustration) properties of the aggregate entity (e.g., size, shape, temperature) in the pursuit of generality. It chooses this path over studying each individual particle and the interactions among the particles (i.e., reductionism). Telescope drawing under CC BY 4.0 license from Science and Education SVG Vectors

9 | CONCLUSIONS

I started by noting that there were two seemingly distinct views of what macroecology is and how and why macroecology should be practised: large scaleness or emergence.[1] I have also noted that both flavours of macroecology share a strong reliance on empiricism based on observational and comparative methods, and that the contrast between macro- and microecology is strongly mirrored in the macro versus micro contrast in evolution and economics, and that maybe macroecology should define scale by levels of aggregation rather than extent.

But as I explored the history of these two views of macroecology and, especially, explored some of the motivations for and implications of these two views, a more complex picture emerged (Figure 6). I believe that this more complex view of macroecology has at least two implications for the future of macroecology.

First, no matter what your entry point to or motivation for or initial view of macroecology, you cannot avoid (owing to the transmutation problem) arriving at the need for an emergent/non-reductionist approach.

Second, I increasingly prefer a (highly complementary) third view or definition of macroecology: "macroecology is the study at the aggregate level of aggregate ecological entities made up of large numbers of particles in the pursuit of generality" (Figure 7). Examples of aggregate ecological entities include species assemblages, communities and a species across its geographical range. Corresponding numerous particles would be species, species and individuals, respectively. Studying at the aggregate level might mean measuring body size distributions, richness or the spatial distribution of a functional trait, respectively.

I believe such a definition captures much of the essence of, and ultimately implies the need for, both the large scaleness and emergence views of macroecology and thus unifies them. Such a definition is also, I believe, highly consistent with the founders' view of macroecology (indeed, it is probably a return to the original foundations). Brown (1999) said, "For me the most critical feature of macroecology is its effort to characterize and explain the emergent statistical phenomena exhibited by systems composed of large numbers of 'particles'." Lawton (1999) talked explicitly about the problem of intermediate numbers and the statistical order that emerges from the scrum. Maurer (1999) was by far the most explicit in laying out such a macroscopic statistical mechanical view. Gaston and Blackburn (2000) describe macroecology as the "attempt to see the wood for the trees". Jim Brown (personal communication) has always seen the prefix macro to imply many particles in addition to large scales. At a minimum, such a view is more consistent with how macroevolution and macroeconomics define themselves as studying aggregate entities (species and national economies, respectively). Lastly, such a definition of macroecology would draw a hard line against an unpacking of the emergent properties of species assemblages into the reductionist pursuit of contingent details of interactions among small numbers of component parts. Specifically, it involves rejecting the notion that macroecology can be pursued at large scales but by reductionist methods. This would require macroecologists to resist the siren song of reductionist claims of superiority that are dominant in ecology. I do not know if that is realistic.

Although rejecting reductionism, this definition does leave open the question of whether the aggregate properties arise primarily from statistical limit theorem laws, from focusing on properties of the particles that show low variance and averages that scale well, thereby avoiding the transmutation problem, or from focusing on basic physical and evolutionary properties of the particles that are so strong they survive the transmutation of scaling. I believe you can find support for all these views within macroecology. Maurer (1999) and Lawton (1999) seem to favour statistical arguments. Brown has increasingly favoured fundamental principles strong enough to survive transmutation (Brown, 1999; also see Mandelbrot, 1963), such as energetics (Brown, 1995). And questions about biomass tend to avoid the transmutation problem (Bar-On, Phillips, & Milo, 2018).

It is far from my desire or ability to decree which view or definition of macroecology is the "right" definition. But I think it is important for participants in the field to be aware of the multiple definitions and the interactions among them. For me (and many others), science has never been about a complete list of facts about the details of the universe. It is about finding generalities. MacArthur (as usual) said it better (1972): "To do science is to search for repeated patterns, not simply to accumulate facts." Which is why I ended up going into macroecology. And it is why I personally find the views of macroecology that involve emergence, pursuit of generality, and large numbers of particles compelling. It is also why, as a macroecologist, I find myself feeling more affinity for macroevolution than for microecology even though nominally the ecology–evolution divide is deeper than the macro–micro divide.

Rather than concluding with the answers, I can only conclude with some questions for you. Is your brain wired in a micro or a macro fashion? If you are a macroecologist, what are you motives for studying large scales? And if you are a macroecologist, which definition of macroecology do you embrace?

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[1] For those who are curious, I believe the first definition is more common in Europe and the second in North America (hence the query about which flavor of macroecology my book would contain). But this is only a weak association. Lawton, for example, is European but was clearly motivated by emergence. I also think that definition of the large-scale view is rapidly increasing (has even risen to a majority viewpoint) in North America.

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