

*New Idea***Beyond individual, population, and community: Considering information, cell number, and energy flux as fundamental dimensions of life across scales****John P. DeLong, Mary I. O'Connor, Van Savage, Tom Luhring, C-Elisa Schaum, and Mike Sears***John P. DeLong, School of Biological Sciences, University of Nebraska – Lincoln, Lincoln, NE, USA 68588**Mary I. O'Connor, Department of Zoology, University of British Columbia, Vancouver, BC, Canada V6T 1Z4**Van Savage, Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA 90095 and Department of Biomathematics, University of California, David Geffen School of Medicine, Los Angeles, CA, USA 90095, and Santa Fe Institute, Santa Fe, NM, USA 87501**Tom Luhring, School of Biological Sciences, University of Nebraska – Lincoln, Lincoln, NE, USA 68588 and Department of Biological Sciences, Wichita State University, Wichita, KS, USA 67205**C-Elisa Schaum, Centre for Earth Systems and Sustainability (CEN) / Institute for Marine Ecosystems and Fisheries (IMF), Hamburg University, 22767 Hamburg, Germany**Mike Sears, Department of Biological Sciences, Clemson University, Clemson, SC, USA 29634***Abstract**

We suggest rethinking ecology as a set of continuous, interconnected dynamics and spatial networks that would represent an alternative framework to the traditional organizational levels—cell, organism, population, community, and ecosystem. We draw on unifying biological theories—information theory, cell theory, and metabolic theories—to propose a continuous space for living systems that avoids epistemological constraints imposed by *a priori* assumptions of discrete levels of biological organization. The discrete levels of organization that ecologists have traditionally envisioned can be viewed instead as coarse-grained, localized groupings within continuous dimensions of information (I), cell number (C), and energy flux (E). Moving from levels of organization to emergent properties of information, cells, and energy flux allows us to illustrate how diverse ecological and evolutionary phenomena—such as allometric and diversity-related scaling patterns, predator-prey dynamics, evolutionary trajectories, and alternative stable states—can be represented within the

same continuum. We suggest that there may be structure within this information-cells-energetic flux (ICE) framework that unifies ecology from the beginning of life to the present and provides a useful lens through which patterns and processes in nature can be viewed.

Key words: Unification of ecology; space-time continuum; ice framework; scale; levels of organization.

Rethinking biological organization

Recent decades have seen increasing efforts to unify ecological understanding across scales (Hubbell 2001, Brown et al. 2004, McGill 2010, Harte 2011). Unifying efforts attempt to bridge gaps or escape the limitations associated with theories and empirical approaches that—often implicitly—emphasize a restricted range of spatial, temporal, or organizational scales (Scheiner and Willig 2008, Marquet et al. 2014). One of the many challenges

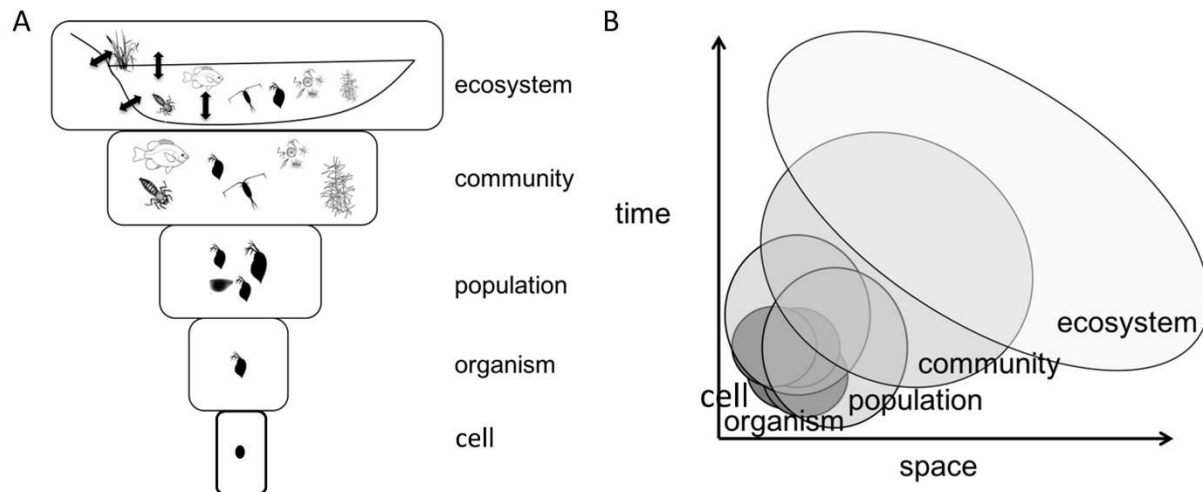


Figure 1. Classic approaches to defining scale in biological systems that are information-free. A) discrete hierarchical levels of organization (cell, organism, population, community, ecosystem), B) traditional concepts of levels of organization are often associated (implicitly) with overlapping spatial and temporal scales,

associated with unifying ecological understanding across scales concerns the concept of scale itself. In physical systems, space and time structure the axes along which physical entities such as galaxies, planets, and grains of sand emerge. Although life also resides within the space-time continuum, space and time alone do not explain biological organization or even the existence of life. Consequently, concepts of biological scale based only on spatial or temporal dimensions cannot be sufficient to capture the full dynamics of life.

Ecological theory generally takes scales of biological organization for granted, focusing on understanding variation in the abundance and distribution of entities within levels of organization (e.g., individuals, species, communities) over space and time (Ricklefs and Schluter 1994, Rosenzweig 1995). Textbooks, journals, and traditional academic disciplines are explicit about the distinction of discrete levels within the biological hierarchy—e.g., cell, organism, population, community, and ecosystem (Figure 1A)—that all play out across different scales of time and space (Figure 1B). This focus on discrete levels obscures the fact that the levels of organization are not strictly hierarchical. For example, animals may simultaneously be an individual, a population of cells, and a community of microbes. Furthermore, these traditional scales lack the integral component of information (O'Connor et al. 2019). We propose that a unified understanding of ecology requires a perspective on scale that emphasizes continuity of biological process and pattern across levels of organization rather than a discrete classification. To that end, we suggest that living systems (any system of life

from a cell to the biosphere) occur within a continuum of three fundamental dimensions of life: information, cell number, and energy flux. Observations on living systems could then be rescaled to these fundamental dimensions and compared, allowing us to collapse disparate patterns into their common patterns, if these exist. In this perspectives piece, we (1) propose that there are three fundamental dimensions of life: information, cell number, and energy flux, (2) suggest some hypotheses about how observations of life could occupy the space demarcated by these dimensions, (3) provide preliminary empirical examples, and (4) suggest ways in which this approach might yield unification across scales in ecology.

A proposal for unification through information, cells and energy flux

To articulate how living systems are structured and function across scales of biological organization, we begin with three observations: (1) Life requires information to guide the flux of energy and the structuring of matter, (2) Life is organized by information (in cells), and (3) Life uses energy to persist and to process information, energy and materials. Any living system contains and processes information of many sorts (e.g., genetic, phenotypic, knowledge, or differences among individuals; for a more thorough review see O'Connor et al. 2019), contains some number of cells, and fluxes some amount of energy (i.e., has a metabolic rate). No living system or aggregation of living things at any level of organization or at any spatial or temporal

scale lacks these three properties. These, therefore, are the fundamental dimensions of life, and combined they make up three axes of what we will call the information-cells-energy flux (ICE) framework. We expand on each axis below.

Information

Information is a fundamental aspect of living systems, and information theory has played a major role in advancing our understanding of life (Margalef 1957, Gatlin 1972, Szathmáry and Smith 1995, Maynard Smith and Szathmáry 1997, Ulanowicz 2001, O'Connor et al. 2019). Biological structures as diverse as genes, interaction networks, and communication systems all contain information, which we define here as the non-random arrangement of energy and matter over space and time (O'Connor et al. 2019, Little et al. 2022). Biological structures process information in myriad ways, from DNA replication to neural signaling to communication across social networks (Frank 2012, Tkačik and Bialek 2016, Gil et al. 2018). Information processing, involving a wide diversity of information storage and transmission systems, is one of the key characteristics of living systems. Information guides the flow of energy, materials, and other information. Without information, and the ability to acquire, store, and retrieve it, energy flows could not be directed toward the maintenance and replication of organisms. For example, messenger RNAs could not be created without the information that guides the production of ribosomes. Thus, molecular information is essential to the basic metabolic functioning of any living system. Information is no less critical at ecological scales of organization, as in the detection of predation risk or the identification of potential mates. Moreover, the ability to gather and store useful information is likely under selection, suggesting that information and its processing systems reflect evolutionary history and the ecological context.

The scale of the information axis can be defined in many ways, including but not limited to the number of alleles or genes, the variation in genes or phenotypes, and the structure of genomes (Jiang and Xu 2010, Sherwin et al. 2017, Wagner 2017). Information in ecological systems can contain meaning (i.e., semiotic information) or indicate distributions and arrangements of states (i.e., syntactic information). Therefore, information also can be estimated in terms of variation (e.g., phenotypic) and diversity of a system (including Shannon entropy), even without specific reference to genetics (Jost 2006, Jiang and Xu 2010, Tkačik and Bialek 2016), as variation is a reflection of the non-random state of matter (O'Connor et al. 2019). None of these units captures all the information in a living system, just as no single unit of energy captures all forms of energy (e.g., kinetic, potential) in a system. Although information refers to

many things and therefore can seem vague and difficult to pinpoint, for our purposes the clear function of information is to guide living organisms toward the furtherance of life.

Cells

Cells are the fundamental unit of organized life. Ecological systems can contain unicellular organisms and many cells operate in a co-dependent manner in metazoans. Cell theory—the idea that all living things are made of one or more cells, cells arise from other cells, and metabolism occurs within cells—is a cornerstone of modern biology (Mazzarello 1999). Cells consist of membranes that maintain a homeostatic environment for information carriers—DNA, RNA—protecting these molecules from environmental decay (Patten 1959, Johnson 1970, Kempes et al. 2017b). We consider cell number to be a scale along an axis that more generally captures the amount of life and the organization of physical materials into living structures, regardless of level of organization. Thus, increasing cell number may represent increasing populations, larger metazoans, or more complex communities, but it also may represent aggregations of cells classifiable as more than one thing (e.g., individual and population). Although cells may vary in size, larger free-living cells often have larger genomes (DeLong et al. 2010), suggesting that cell size variation may be seen at least in part along the information axis instead of the cell number axis. However, variation in genome size is less related to adult body mass than propagule size (Glazier 2021), suggesting less covariation of information and cell number in metazoans.

Energy flux

A third key feature of life is metabolic power. Metabolic rate reflects the biochemical work done in the process of acquiring, transforming, and allocating resources toward growth, reproduction, and survival (i.e., the ‘fire of life’; Kleiber 1961). Metabolic rate is a unifying currency of all the work that organisms do and is the central element of the Metabolic Theory of Ecology (Brown et al. 2004) and Dynamic Energy Budget theory (Kooijman 2000). Although cells contain an amount of energy in their molecular bonds, it is the *flux* of energy that allows cells to process information and build more cells. Because metabolic rate is measured with respect to a particular time frame, the choice of time scale (i.e., day, year, or generation time) may influence observed patterns of energy flux in living systems. Increasing metabolic rates may reflect, among other things, larger cells, larger metazoans, bigger populations, or more diverse communities, as well as abiotic factors such as temperature.

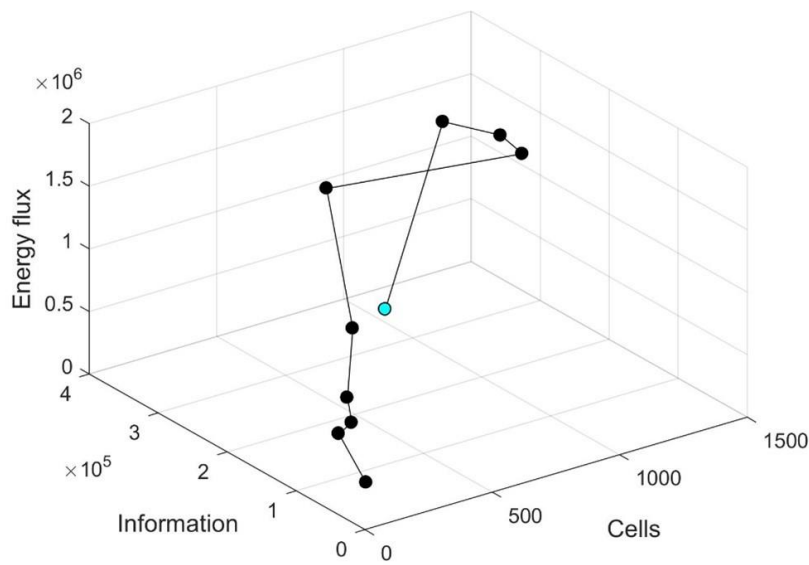


Figure 2. A) The dynamics of a *Didinium-Paramecium* predator-prey system through one population cycle, starting at the blue point. As the total number of cells changes in the system, so does the overall flux of energy. *Didinium* cell volume also varies through time, as does individual variation in cell volume. Here we have plotted time series of total number of cells (*Didinium* plus *Paramecium*), the total metabolic rate assuming density dependent metabolic rates, and the standard deviation in cell volume as a measure of information.

Life in ICE dimensions

All samples of life—from free-living cells to the biosphere—have some number of cells, process information, and flux energy. Thus, any living system can be rescaled to these three dimensions and visualized in the space they define. Though there clearly are other axes of variation in living systems, we suggest that fundamental interactions between cell number, energy flux (metabolic rate) and information processing can constrain or guide the structure and dynamics of living systems. Furthermore, all living systems display changes through time, for example through reproduction and growth (a change in cell size and/or number and information if cell differentiation occurs), seasonal variation in resource acquisition (a change in energy flux), and through mutations, learning and evolution (a change in information). Thus, we view the ICE dimensions as the fundamental ecological theater (Hutchinson 1965) for the dynamics of living systems, from growth to population cycles to succession.

As an example, consider the classic *Didinium-Paramecium* predator-prey system. The exploitative interaction between these two ciliates generates dynamic changes in abundance, traits, and trait variance through time (Figure 2A) (Gause 1935, Luckinbill 1973). Using experimental data (DeLong et al. 2014), we illustrate these dynamics by plotting the total number of cells (*Didinium* and *Paramecium* cells combined), estimated metabolic rate (total cell volume-and density dependent metabolic rates), and the standard deviation of cell volume (taking trait variance as a form of information; see above and Frank 2009). Thus, a pattern that is

normally seen as a cycle of two populations in time also can be understood as a three-dimensional cycle of information, cells, and energy flux. We emphasize that exploitative interactions among species can generate oscillations in abundance of many species through time (Hudson et al. 1998, Krebs et al. 2001), and even though such systems may vary widely in mechanisms of interactions, rates of evolution, and virtually every other natural history detail, all of those systems could be plotted on the same axes of information, cells, and energy flux. Our perspective is that comparing ecological interactions such as predator-prey cycles in the ICE dimensions could reveal commonalities and further the goal of unification in ecology.

An interesting challenge to the ICE framework are life forms that do not have metabolic power, such as viruses. We cannot plot viruses in the ICE dimensions because they do not have their own metabolism and are not defined as cells (although virions may have capsids and/or membranes that similarly shield them from the environment). A virus's host cell, however, exists in the ICE dimensions. As molecular parasites, virions occur only along the information axis. Therefore, the process of infection is inherently one of changing the information in a host cell. After infection (and if they are not latent), the host cell changes, including both in its information content (the addition of new genetic information) and power (up- or down-regulation of photosynthesis or other processes). In this way, both free-living cells and metazoans are likely to move in the ICE space upon infection. Thus, viruses (or plasmids) cannot be not placed in the ICE dimensions on their own, but they can alter the position of living systems in the space.

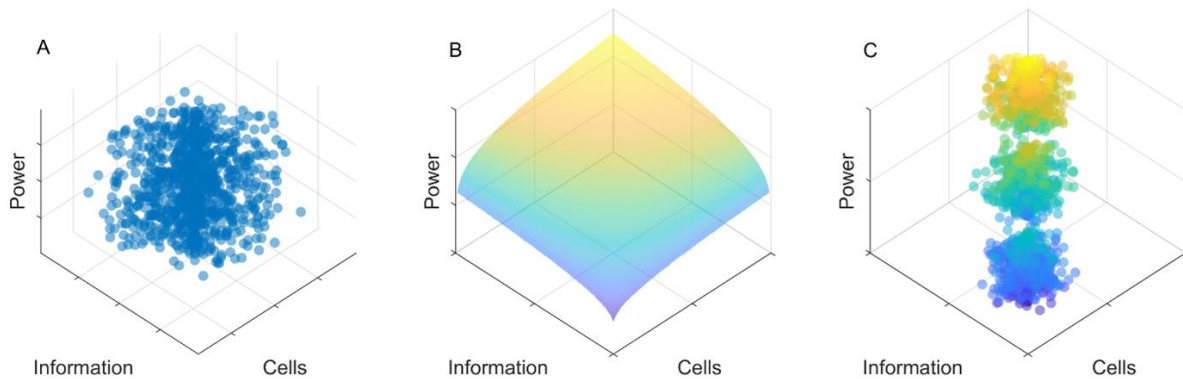


Figure 3. Three hypotheses about how measures of information, cells, and energy flux would aggregate. A. The ICE cloud hypothesis, B. The ICE sheet hypothesis, and C. The ICE clusters hypothesis.

Structure and dynamics in the ICE dimensions

The position of living systems in the ICE dimensions may generate deeper insights into the continuity of ecological systems and perhaps open a door to a way of unifying ecology across scales. We offer three hypotheses for how ecological and biological systems might populate this space.

The ICE cloud hypothesis

Observations of information, cell number, and energy flux form a cloud, occupying most possible combinations (Figure 3A). Only hard physical constraints define boundaries of the cloud: minimum energy content of an information-carrying structure, for example. Within the domain of possible states, there are no strong constraints, attractors, or organizing forces that *a priori* determine which combinations of cells, information, and power are likely to arise or persist in nature.

The ICE sheet hypothesis

Alternatively, cells, information, and energy flux aggregate loosely along a surface originating at the intersection of one cell, the minimum amount of information necessary to power a cell, and the minimum power used by a cell (Kempes et al. 2017a). The surface increases away from this origin (Figure 3B). This surface could arise because of two simple relationships between energy, information and cells. The first is that energy flux increases with the number of cells, so the sheet should increase on average as more cells characterize a system. Second, additional information creates the potential for additional biochemical pathways to develop, expanding the ability of organisms to do work (DeLong et al 2010),

so energy flux should increase with information. Now, as the number of cells increases, the diversity among cells (information) has greater potential to increase as well, allowing the surface to expand along the information axis and the cell axis simultaneously, generating a surface within the ICE framework. The ICE sheet likely would be thick, with that thickness representing both variation in average energy flux and changing energy flux through time, rather than a thin two-dimensional sheet.

The ICE cluster hypothesis

A third possibility is that there may be multiple attractors forming clusters of points that represent levels of organization and/or major evolutionary transitions (Figure 3C). More stable or persistent combinations of information, cells, and energy flux may emerge as high-density regions in this space. Even if such high-density regions exist, this hypothesis allows most other regions of the space to be populated, revealing a much more continuous (in three dimensions) organization of life in the biosphere than our traditional discrete hierarchy would suggest. The clusters could look a bit like loose galaxies if there are attractors within the ICE dimensions, with individual free-living microbes clustering together, for example, and a jump to a cluster of free-living individual metazoans. Moreover, clusters could arise at different hierarchical scales given similarity of power, cell number, and information. For example, populations of like taxa might cluster together given that the energetic equivalence rule suggests similar power and the inverse relationship between body size and abundance (Damuth 1981) could lead to a similar total cell count across population. Yet we know little about how information might vary across populations, leaving the location of populations in the ICE dimensions still uncertain.

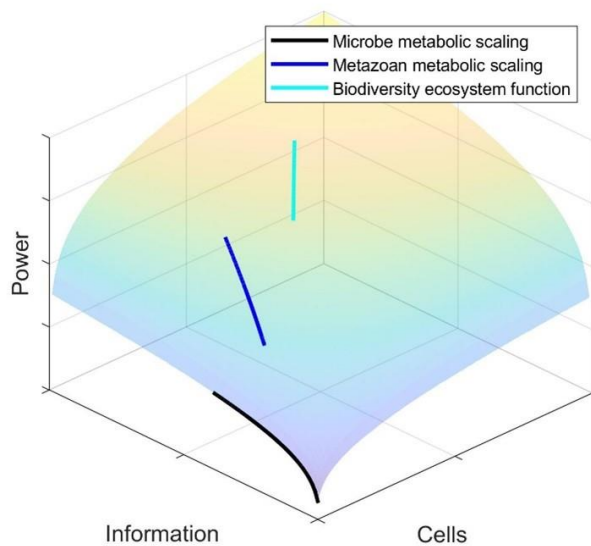


Figure 4. Three relationships connecting energy flux to organisms: the scaling of metabolism with body mass (and hence genome size) in bacteria (black line), the scaling of metabolic rate for metazoans (blue line), and the biodiversity-ecosystem function relationship (turquoise line, see text for more information).

The potential for unification

One desired outcome of unification in ecology is to explain patterns and processes across scales in a single unified theoretical framework. Recasting observations from different levels of organization or different systems into their fundamental dimensions – information, cell number, and energy flux—could promote such understanding by highlighting fundamental differences and similarities across systems or spatial and temporal scales. The ICE framework allows us then to test hypotheses about the scale dependence of major biological theories and laws and to evaluate how potentially divergent patterns might coalesce within a single continuum.

For example, allometric scaling relationships linking energy flux and body size and saturating relationships between ecosystem function and species richness are major patterns observed at the individual and community levels of organization, respectively (West et al. 1997, Loreau and Hector 2001, DeLong et al. 2010, Cardinale 2011). Although these two types of patterns appear to emerge from different processes, they could appear very similar within the ICE dimensions. This is because increasing body size (Neufeld et al. 1998) and species richness can both increase cell number (through additional cell division for individuals and the addition of more individuals in higher richness communities) and information (through more cell differentiation within individuals and species richness within communities). For example, the scaling of metabolism with body mass (and hence genome size) in bacteria could be a curve that runs along the edge of the ICE sheet (remember Figure 3B), where cell number is constant at one but information

and metabolic rate increase together (Figure 4, black line). For metazoans, in contrast, both cell number and information vary with body mass, so this scaling relationship could cross the ICE sheet transversely (Figure 4, blue line). Finally, the biodiversity-ecosystem function relationship connects energy flux to species diversity, which comes with both an increase in the number of cells (more individuals) and number of taxa (more information), creating a curve that occurs farther up the ICE sheet (Figure 4, turquoise line). Thus, all three patterns—fundamentally different seen through the lens of levels of organization—could show up in the ICE dimensions as similar arcs increasing in power with increasing cell number and information. Whether such relationships really do look similar in the ICE dimensions is unknown, but if such curves showed continuity of structure in this way, it would suggest that what we once viewed as discrete, unrelated patterns, may actually be unified within a single framework of fundamental dimensions.

The ICE framework may allow additional advances in unification across many ecological dynamics and patterns. Some other possibilities include: (1) The ontogeny of metazoans involves the addition of cells of increasing tissue differentiation and additional metabolism, suggesting that ontogenetic growth curves could occur within the ICE dimensions as similar trajectories. (2) Predator-prey cycles all involve changes in cell number, total system power, and potentially information, but since individual predator and prey have vastly different cell numbers, one could imagine a cone of cycles expanding from single-celled systems to larger metazoan systems. (3) Succession in communities involves changes in species type and function, and since

these changes can be somewhat predictable, it may be that successional changes in the ICE dimensions proceed along similar trajectories. (4) Major evolutionary transitions involve jumps in the way individual organisms interact to form new organisms. It is possible then that different transitions (e.g., the evolution of eukaryotes, metazoans, or social organisms) show jumps in their position in the ICE dimensions due to changes in power, cell number, or information across the transitions. (5) We also might imagine that some combinations of cells and information do not function well and might create pits and valleys in the surface, with high points in the sheet representing likely states (e.g., alternative stable states) that a system could attain (Odum 1995, Hall 2004).

The three dimensions of information, power, and cell number may not be fully independent. We think it probable, for example, that information is likely to increase as cell numbers increase, either through the increase of genetic information (genome size, number of active transcripts), the more random state of molecules across the cell, and the increased diversity of structures distributed across the cell. This could be through both differentiation among cells in a growing multicellular organism and the addition of cells that contain different information (e.g., another species) within a growing community. However, such a relationship is not strictly required. A growing population of genetically identical cells (clones) could expand along the cell and energy flux axes with changes in information that would depend on how it is measured. For example, there may be no change in the information stored in the genome (semiotic information) but change in the information measured as variation in states (syntactic information). In nature, such expansion might be unlikely, given the eventual emergence of a mutation with enough DNA replication or the invasion by another cell type. In this way, the dimensions of ICE may not be as cleanly distinct and independent as three dimensions of space in which all locations are equally accessible.

An open question about the ICE framework is whether there are general mathematical links among the three dimensions that guide the dynamics of living systems. A particular challenge to such a generalized mathematical framework might come from the variety of forms of information that could be guiding cells to conduct work. Nonetheless, causal connections exist that could link the dimensions: energy flux powers the creation of new cells given information, information is used by cells to flux energy, and cells generate more information (in its various forms) as they grow, divide, or mutate. Furthermore, population growth can add or remove cells, simultaneously altering energy fluxes and information, which could then further alter demographics. How to connect these dimensions, or whether different systems require different connections to

describe their dynamics, is not clear at this point. A potentially fruitful way forward is to recast dynamics from multiple systems that can be described mathematically in terms of abundances (e.g., the *Didinium-Paramecium* cycle) into their corresponding levels of information, cell number, and energy flux and determine whether the dynamics in the ICE framework can be described with common models. Alternatively, the ICE framework represents merely the full outline of Hutchinson's ecological theater, with the dynamics driven by forces other than information, cell number, and energy flux.

One potential critique of our proposal is that there already exists a wealth of patterns unified by variation in body mass (Peters 1983, Calder 1996, Brown et al. 2004), making the ICE framework redundant. Indeed, body mass should be tightly linked to the number of cells, even with variation in the mass of individual cells, making the cell axis a *de facto* body mass and biomass axis. However, we emphasize that cells are a more fundamental unit of life than units of mass such as grams. Cells contain the structures that facilitate power and contain information, and they are the core replicating unit of life. Even with cell differentiation, conjugation, and sex, cell division is the fundamental process through which life generates more life. Furthermore, we suggest that the tight link between number of cells and mass would likely make cell number equally useful as an allometric predictor, albeit one that might be harder to measure than weighing (at least some kinds of) individuals.

Conclusion and prospectus

We propose that a unified understanding of ecology requires a perspective on scale that emphasizes continuity of biological process and pattern across levels of organization in a manner that is formally consistent with first principles. Such an approach would allow study of biological organization without imposing discrete and subjective coarse groupings such as populations or communities and their arbitrary relationships to spatial and temporal scales. We propose, as a first attempt, that information, cell number, and energy flux (ICE) represent the fundamental dimensions of life and thus are unifying, continuous scales for living systems. We further suggest that this ICE framework has the potential to reveal deeper insights about ecology beyond scales. Although we recognize that other frameworks are possible (e.g., allometric scaling, Metabolic Theory of Ecology (Brown et al. 2004), or the Maximum Entropy Theory of Ecology (Harte 2011)), we argue that ICE framework may facilitate the understanding similarities of pattern and process across living systems.

Finally, many current approaches assume a focus on a particular level of biological organization and a stable

organizational structure—an individual, a population, a community—and from this focal level of organization, dynamics and patterns are expected to ‘scale’ up or down to other levels. Our proposal avoids these hierarchies altogether, and allows us to ask how life is structured along fundamental axes that transcend traditional levels of organization. It remains a challenge to measure living systems in terms of their ICE dimensions, but we suspect that as we populate the ICE framework with data from many systems, new patterns will emerge that illustrate what truly unifies life.

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