THE INFORMATIONAL THEORY OF BIOLOGICAL INDIVIDUALITY: HOW ORGANISMAL BOUNDARIES ARISE FROM INFORMATION FLOW RATHER THAN PHYSICAL MEMBRANES

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Abstract: Where does one organism end and its environment begin? The default answer in much of biology is spatial: the boundary is the outermost membrane, the skin, the cell wall. This article argues that the membrane is a poor guide to individuality and that the boundary of an organism is better located where information flow closes on itself. I develop the Informational Individuality Criterion (IIC), a three-axis operationalization that scores any candidate system along informational closure (the contrast between internal predictive mutual information and boundary-crossing mutual information), integrated information (the irreducibility of the system's cause–effect structure), and constraint-based autonomy (the organizational closure of the constraints that maintain the system). On this account, the organismal boundary is the closed surface that maximizes a composite individuality functional, not the surface drawn by lipids or cuticle. I test the criterion on three cases that break the membrane intuition in opposite directions: the mammalian holobiont, in which many membranes enclose one informational individual; the multinucleate syncytium, in which one membrane encloses several partly autonomous informational sub-individuals; and the colonial siphonophore, in which many zooid membranes are subordinate to a single integrated colonial self. Across all three, the informational boundary systematically diverges from the physical membrane, and I quantify that gap with a Membrane–Information Divergence diagnostic. The upshot is that individuality is graded, sometimes nested, and frequently displaced from the membrane — an outcome that membrane-based criteria cannot represent but that an informational criterion renders precise and, in principle, measurable.
Keywords: *biological individuality, information flow, integrated information, causal closure, autonomy, holobiont, syncytium, colonial organisms.*

INTRODUCTION

The question of biological individuality sits at an odd crossing point between empirical biology and philosophy of biology, and it has grown more urgent as the tidy picture of the organism as a membrane-bounded genetic unit has come apart. Microbiome research has shown that a mammal is, functionally, a consortium; developmental biology has shown that gene expression is redirected by mechanical and bioelectric fields that ignore cell boundaries; and evolutionary theory has multiplied the levels at which selection and inheritance operate (Pradeu, 2019; Levin, 2021; Bourrat, 2019). Yet across these shifts one habit persists: when pressed to say where an organism stops, biologists point to a surface — the plasma membrane, the epithelium, the cuticle. The membrane is treated as the natural edge of the self. This article takes that habit as its target.

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My claim is that the membrane is at best a rough proxy for individuality and at worst actively misleading, because the property that actually makes a system one thing rather than many, or many rather than one, is not the presence of a shared physical envelope but the structure of information flow within and across the candidate boundary. A system is an individual to the degree that its internal states predict one another more than they predict, or are predicted by, states outside it — that is, to the degree that information closes on itself. This intuition is not new in outline; it is implicit in the information theory of individuality developed by Krakauer and colleagues (2020), in the Markov-blanket formalism applied to living systems (Palacios et al., 2020), and in the organizational tradition that defines autonomy through closure of constraints (Bich et al., 2020). What has been missing is a single criterion that combines these strands and is put to work against the cases where the membrane and the information boundary most sharply disagree.

The central research question of this article is therefore the following: if we stop assuming that the organismal boundary coincides with a physical membrane and instead locate it where informational closure is maximal, does the resulting account of individuality improve on the membrane account, and what does it predict for systems in which membranes and information flow come apart? From this question I derive three hypotheses. The first is that a well-defined informational boundary exists for a wide class of biological systems and can be operationalized without reference to any physical envelope. The second is that this informational boundary systematically diverges from the physical membrane in both directions — that some systems have many membranes but one informational individual, and others have one membrane but several informational individuals. The third is that individuality, once defined informationally, is graded and often nested rather than binary, so that the same biological material can support individuals at more than one scale simultaneously.

The original contribution of this article is the Informational Individuality Criterion (IIC): a three-axis operationalization — informational closure, integrated information, and constraint-based autonomy — that locates the organism's boundary at the surface of maximal informational closure, together with a Membrane–Information Divergence diagnostic that measures how far that surface lies from the physical membrane. Unlike prior work, which has advanced each of these three axes separately and has largely argued about individuality in the abstract, the IIC binds them into a single scoring procedure and applies it to three systems — holobionts, syncytia, and colonial organisms — that break the membrane intuition in different directions. The point is not to add another verbal definition of the individual to an already crowded field, but to offer an instrument that is explicit enough to be scored, compared, and disputed. I should say at the outset that the instrument is heuristic rather than fully computed; its values are reasoned estimates drawn from the empirical literature, and their role is to structure disagreement, not to end it.

A brief note on scope will prevent misunderstanding. I am not claiming that membranes are unimportant. Membranes do real causal work: they concentrate reactants, hold electrochemical gradients, and gate transport. The claim is narrower and, I think, more defensible — that membranes are not what individuality consists in, and that treating the membrane as the criterion of the self produces systematic errors precisely in the cases biologists find most puzzling. Where the membrane and the informational boundary coincide, as they do for a free-living bacterium or a solitary animal, nothing is lost by using the membrane as shorthand. Where they diverge, the membrane misleads, and only the informational criterion tracks the individual.

The article proceeds as follows. After this introduction, a combined literature review and methodology section reconstructs the three research traditions the IIC draws on and specifies how the criterion is scored. A separate results section then presents the three-axis profiles and the divergence diagnostic for the three test systems without interpretation. Three analytical

sections follow, treating in turn the formal structure of the informational boundary, the holobiont and colonial cases where membranes over-divide the individual, and the syncytial case where the membrane under-divides it. A concluding section answers the three hypotheses, restates the contribution, and marks the limits of what a heuristic criterion can settle.

LITERATURE REVIEW AND METHODOLOGY

Literature Review

The most direct precedent for the present argument is the information theory of individuality proposed by Krakauer, Bertschinger, Olbrich, Flack and Ay (2020), who define an individual as a system that propagates information from its past to its future while remaining partially decoupled from its environment. Their key move is to make individuality a matter of degree and to allow for several distinct types — from strongly autonomous organisms to environmentally scaffolded and colonial forms — depending on how information is partitioned between system and surroundings. This reframing dissolves the demand for a sharp physical edge: an individual is wherever information is maximally self-contained, and that locus need not respect any membrane. The account has been influential precisely because it replaces a substance question with an information-partition question, and it supplies the formal backbone on which the first axis of my criterion is built.

A parallel formalism arrives from the free-energy principle and its use of Markov blankets. Palacios, Razi, Parr, Kirchhoff and Friston (2020) show how a statistical boundary — a set of states that renders internal and external states conditionally independent — can be defined at multiple nested scales, so that cells, tissues and organisms each carry their own blanket. The attraction of this framework is that it gives a precise, if abstract, sense in which a system can be individuated by conditional-independence structure rather than by anatomy. It has, however, drawn sharp criticism. Bruineberg, Dołęga, Dewhurst and Baltieri (2022) argue that the Markov blanket has been quietly reinterpreted from a modelling convenience into a real physical boundary, and that this slide smuggles in metaphysical commitments the mathematics does not license. Raja, Valluri, Baggs, Chemero and Anderson (2021) press a related worry about the scope of the construct. I take these critiques seriously and, for that reason, do not rest the criterion on Markov blankets alone; the blanket contributes to the informational-closure axis but is disciplined by the other two axes and by the demand that the boundary do explanatory work in concrete cases. Ciaunica, Levin, Rosas and Friston (2023) show, in the prenatal case, how shared and nested blankets can model an individual that is neither fully one nor fully two — a structure my syncytial and holobiont analyses will need.

The second axis draws on integrated information theory, which supplies a measure of how far a system's cause–effect structure is irreducible to the sum of its parts. Recent formal work has extended the measure from single mechanisms to whole systems: Marshall and colleagues (2023) define system integrated information, while Barbosa, Marshall, Streipert, Albantakis and Tononi (2020) introduce a measure of intrinsic information and, in a companion paper, of mechanism-level integrated information (Barbosa et al., 2021). Whatever one makes of the theory's more ambitious claims about consciousness, its core quantity is exactly what an account of individuality needs: a way of asking whether a candidate boundary encloses one integrated cause–effect structure or several loosely coupled ones. I use integrated information in this restricted, individuational sense, not as a theory of experience.

The third axis comes from the organizational tradition in theoretical biology, which defines biological autonomy through closure of constraints — the condition in which the constraints that

channel a system's processes are themselves collectively produced and maintained by those processes. Bich, Mossio and Soto (2020) work this out in detail for glycemic regulation, showing how organizational closure yields a principled sense of what belongs to the system. Virenque and Mossio (2023) extend the framework toward a theory of agency. This tradition matters for my purposes because informational closure alone is not sufficient: a whirlpool exhibits informational self-containment without being an individual in any biological sense. What distinguishes the organism is that its informational closure is underwritten by a self-maintaining organization of constraints, and the autonomy axis captures that difference.

Against these formal traditions stands a rich literature on individuality in the philosophy of biology that is more sceptical of any single criterion. Pradeu (2019) argues from immunology that the organism is defined not by genetic homogeneity but by the reach of an active immune system that continuously negotiates self and nonself; on this view the boundary is dynamic and immunological rather than anatomical. Boehm, Morimoto, Trancoso and Aleksandrova (2023) trace how self/nonself discrimination itself evolved out of genetic conflict, which suggests that even the immune boundary is a contingent achievement rather than a given. Trappes (2024) reminds us that individuality debates are shaped by practices and interests, warning against treating any one criterion as the last word. Kearney and Rieppel (2022) push a process-ontological alternative in which organisms are stabilized activities rather than bounded things — a view congenial to mine, since a stabilized activity is exactly what a closed information flow is. I read these contributions not as rivals to be defeated but as constraints on what an adequate criterion must do: it must be graded, dynamic, and answerable to the concrete biology of hard cases.

The hardest cases cluster around three phenomena. The holobiont — a host together with its microbial symbionts — has become the paradigm challenge to genetic individuality. Suárez (2020) defends a stability-of-traits conception on which the holobiont is an evolutionary individual when host and microbiome jointly maintain stable traits across generations, while Roughgarden (2023) builds a population-genetic theory of the hologenome, and Devanesan (2025) asks pointedly whether the physiological individual and the evolutionary individual coincide in the holobiont — often they do not. Horizontal gene transfer complicates the picture further by moving heritable information across lineage boundaries, a process whose reach in extremophilic archaea has been examined in this journal by Subotić (2025). The second phenomenon, the syncytium, has received less philosophical attention but is biologically sharp: a single continuous cytoplasm may contain many nuclei running semi-independent programs, as recent work on condensate-patterned local translation in multinucleate cells demonstrates (Geisterfer, Jalihal, Cole & Gladfelter, 2026). The third, colonial organisms such as siphonophores, presents the mirror image: physically distinct zooids, each membrane-bounded, function as organs of a single swimming individual (Sutherland, Gemmell, Colin & Costello, 2019). Each phenomenon breaks the membrane intuition, and each breaks it differently.

Two further bodies of work inform the criterion at its edges. Developmental bioelectricity, as synthesized by Levin (2019, 2021, 2023), shows that the functional boundaries of a "self" are set by bioelectric signaling networks that establish which cells share goals and memories, and that these boundaries can be experimentally enlarged or shrunk without changing anatomy — a striking empirical demonstration that the informational self and the anatomical body are separable. Fields and Levin (2019) frame multicellularity itself as a solution to a collective prediction problem, which dovetails with the information-partition view. And the thermodynamics of information (Kolchinsky & Wolpert, 2021) grounds the whole enterprise physically, showing that information processing has determinate energetic costs, so that an informational boundary is not a free-floating abstraction but a structure with a thermodynamic price. Related evolutionary work on transitions in individuality (Doulcier, Takacs & Bourrat, 2023; Bourrat, 2019) and on

reciprocal organism–environment causation (Baedke, Fábregas-Tejeda & Prieto, 2021) and niche construction (Trappes, 2021) situates the graded, nested individuality I will defend within a broader shift away from fixed units. This journal has also published relevant adjacent work on the individuality of the genome itself (Markovski, 2024), on transgenerational epigenetic information (Souza Mendes, 2024), and on how mechanical forces at the nuclear envelope redirect gene expression (Bokuchava, 2025) — the last a particularly apt reminder that even inside a single cell, informational control and physical boundary are distinct.

What the field lacks is not ideas but integration. The information-partition, integrated-information and autonomy traditions rarely speak to one another, and the philosophical individuality literature rarely commits to a scorable procedure. The methodology that follows attempts both.

Research Methodology

The study is conceptual and comparative. It does not report new empirical measurements; it constructs a criterion and applies it to three well-documented classes of system, drawing all parameters from peer-reviewed literature published from 2019 onward. The first methodological component is the specification of the Informational Individuality Criterion as a function of three axes, each scored on a normalized scale from 0 to 1.

The first axis, informational closure (C), formalizes the contrast between how strongly a candidate system's states predict one another and how strongly they are entangled with external states. Following the logic of Krakauer and colleagues (2020) and the conditional-independence structure of Palacios and colleagues (2020), C approaches 1 when internal predictive mutual information dominates boundary-crossing mutual information, and approaches 0 when the candidate boundary is informationally porous — when knowing the outside tells you as much about the inside as the inside does. The second axis, integrated information (Φ), captures whether the enclosed cause–effect structure is irreducible, using the system-level construct of Marshall and colleagues (2023); a high Φ marks a single integrated individual, a low Φ a mere aggregate of weakly coupled parts. The third axis, constraint-based autonomy (A), scores the degree to which the system's boundary is maintained by organizational closure of constraints in the sense of Bich, Mossio and Soto (2020); A distinguishes a self-maintaining organism from a merely informationally coherent pattern such as a vortex.

From the three axes I compute a composite individuality score I as their weighted combination, and — this is the diagnostic that does the comparative work — a Membrane–Information Divergence (MID), defined qualitatively as the direction and magnitude of the gap between where the physical membrane draws the boundary and where the composite score I peaks. MID takes one of three values: coincident (membrane and informational boundary agree), over-divided (membranes are more numerous than informational individuals, so the membrane under-counts the self), or under-divided (one membrane encloses several informational individuals, so the membrane over-counts the self). I chose this three-way scheme rather than a single signed number because the interesting biology lies in the direction of divergence, not merely its size, and a signed magnitude would flatten that distinction.

The scoring rubric is deliberately explicit so that it can be contested. A value near 1 on any axis is assigned when the literature provides direct evidence that the property holds at the relevant scale; a value near 0.5 when evidence is partial or the property is contested; a value near 0 when the property is structurally absent. I assign the scores myself, from the cited literature, and I regard this single-coder design as the principal weakness of the method — a weakness I flag now and return to in the limitations. The final methodological component is a sensitivity check: I vary the axis weights within a plausible band and confirm that the qualitative divergence classification for

each system is stable under that variation. Numbers presented in the results should be read as ordered estimates whose function is to make the argument disputable, not as measured constants. Their precision is a convenience of exposition, not a claim to have quantified individuality to two decimal places.

RESEARCH RESULTS

Applying the Informational Individuality Criterion to the three test systems yields findings that fall into three blocks: the axis profiles, the composite scores with their divergence classification, and the sensitivity analysis. Table 1 collects the axis values and the membrane–information divergence for each system.

The holobiont, taken as a mammalian host together with the stable core of its microbiome, scores moderately high on informational closure ($C \approx 0.72$), because host physiology and the resident microbial community exchange a dense internal traffic of metabolic and immune signals that binds them more tightly to one another than to the outside environment (Pradeu, 2019; Suárez, 2020). Its integrated information is moderate ($\Phi \approx 0.60$), reflecting genuine but incomplete integration between host and microbial subsystems, and its autonomy is moderate-to-high ($A \approx 0.65$), since the joint system maintains stable traits across perturbations (Devanesan, 2025). The composite score $I \approx 0.66$ identifies a real informational individual — but that individual encloses billions of separate microbial membranes plus the host's own cells. The membrane count is enormous; the informational individual is one. The divergence is therefore over-divided: membranes far outnumber selves.

The syncytium, exemplified by a multinucleate fungal or plasmodial cell, inverts this relationship. Its informational closure is only moderate ($C \approx 0.55$), because the shared cytoplasm does couple the nuclei, but recent evidence shows that local translation and cytoplasmic domains are patterned by condensates so that different nuclear neighborhoods run partly independent programs (Geisterfer et al., 2026). Integrated information is moderate ($\Phi \approx 0.68$) but, crucially, is not maximal at the level of the whole cell: sub-cellular domains retain their own weak cause–effect cores. Autonomy at the whole-cell level is moderate ($A \approx 0.58$). The composite score for the whole syncytium, $I \approx 0.60$, is real but conceals internal structure, because the informational analysis locates several partial individuals inside one continuous membrane. Here the divergence is under-divided: one membrane, several informational selves nested within it.

The colonial siphonophore presents the cleanest case of membrane under-counting. Its zooids are separate, each membrane-bounded, yet functionally specialized as swimming bells, feeding polyps and reproductive units serving one integrated animal (Sutherland et al., 2019). Informational closure is high ($C \approx 0.80$) because the colony's coordinated locomotion and division of labor require dense inter-zooid signaling that dwarfs the colony's coupling to its surroundings. Integrated information is high ($\Phi \approx 0.75$), and autonomy is high ($A \approx 0.78$), since the colony maintains and regenerates its organization as a whole. The composite score $I \approx 0.78$ is the highest of the three systems, and it attaches to an entity composed of many membranes. The divergence is again over-divided, and more strongly than in the holobiont: the informational individual is unambiguously the colony, not the zooid.

Two patterns emerge across the three systems taken together. First, the composite individuality score and the membrane count are essentially uncorrelated: the siphonophore, with the most membranes among the strongly integrated cases, is the strongest informational individual, while the syncytium, with a single membrane, is the weakest. Second, divergence runs in both directions — membranes over-count the self in the syncytium and under-count it in the holobiont and the colony — which means no monotonic correction ("always look one level up" or "always look

one level down") could reconcile the membrane with the informational boundary. Only a criterion that computes the boundary directly, as the IIC does, recovers the right individual in all three cases.

The sensitivity analysis supports the robustness of the divergence classifications. Varying the three axis weights across the range from 0.2 to 0.5 each, subject to their summing to one, leaves every system's divergence class unchanged: the holobiont and colony remain over-divided, the syncytium remains under-divided. To flip the syncytium out of the under-divided class, one would have to weight whole-system integrated information so heavily, and sub-domain structure so lightly, that the documented independence of cytoplasmic domains (Geisterfer et al., 2026) would be defined away rather than assessed. The classifications thus do not depend on fine-tuned weights, though the exact composite values obviously do.

Axis / diagnostic	Holobiont (host + microbiome)	Syncytium (multinucleate cell)	Colonial organism (siphonophore)
Informational closure (C)	0.72	0.55	0.80
Integrated information (Φ)	0.60	0.68	0.75
Constraint-based autonomy (A)	0.65	0.58	0.78
Composite individuality (I)	**0.66**	**0.60**	**0.78**
Membrane–information divergence	Over-divided (many membranes, one self)	Under-divided (one membrane, several selves)	Over-divided (many membranes, one self)

Table 1. Three-axis Informational Individuality profiles (0–1, heuristic estimates) and membrane–information divergence for three test systems.

Note. Values are reasoned estimates drawn from the cited literature; the scoring procedure is described in the Research Methodology section. Φ denotes relative system-level integrated information. Divergence class, not the exact composite value, is the comparative result.

THE INFORMATIONAL BOUNDARY: WHAT IT IS AND WHY THE MEMBRANE IS NOT IT

The results invite a more careful statement of what an informational boundary is and why it should be preferred to the membrane. An informational boundary is a closed surface in the space of a system's components such that predictive mutual information is dense within it and sparse across it. Where such a surface exists and is stable, the states inside form a natural kind for purposes of prediction and control: intervening on one internal variable propagates preferentially to other internal variables, and the outside can be summarized, from the inside's point of view, by a low-dimensional interface. This is the content shared by the information-partition account of Krakauer and colleagues (2020) and the conditional-independence account of Palacios and colleagues (2020), stripped of the further and more contentious claim that such a surface must be a Markov blanket in the strict statistical sense. I deliberately keep the weaker commitment, because the Bruineberg critique (2022) shows that the stronger one imports metaphysics the formalism cannot pay for.

Why prefer this surface to the membrane? Because the membrane and the informational boundary answer different questions. The membrane answers a question about material continuity: which molecules are enclosed by a lipid bilayer. The informational boundary answers a question about causal and predictive integration: which states form one self-maintaining, self-predicting whole. These questions have no general reason to receive the same answer, and in the hard cases they do not. A membrane can enclose loosely coupled domains that predict one another only weakly, as in the syncytium; and dense informational integration can span many membranes, as in the colony and the holobiont. Treating the membrane as the criterion of the self is thus a

category error dressed as an observation — it mistakes a fact about material packaging for a fact about individuality.

There is a deeper reason the informational boundary is the right one, and it is functional. What we care about when we individuate organisms — for physiology, for medicine, for evolution — is which system acts as a unit: which system has interests that can be served or thwarted, which system responds to perturbation as a whole, which system is the bearer of adaptations. All three of these are informational and organizational properties, not material ones. Levin's experimental work on developmental bioelectricity makes the point vividly: by altering the bioelectric signaling that couples cells, one can change which cells count as parts of the same self, enlarging or fragmenting the functional individual while leaving every membrane intact (Levin, 2019, 2021). If the self can be moved without moving a single membrane, then the self was never the membrane in the first place. The informational criterion simply makes explicit what these experiments already show.

It is worth being candid about a limit of the argument here. Informational closure is necessary for individuality but not sufficient, which is exactly why the criterion has three axes and not one. A hurricane, a convection cell, and a candle flame all exhibit a degree of informational self-containment, yet none is an organism. What they lack is the third axis: their internal coherence is not underwritten by a closure of constraints that the system itself produces and maintains (Bich et al., 2020; Virenque & Mossio, 2023). The organism differs from the vortex not in having a sharper informational boundary — the vortex's can be quite sharp — but in that the organism builds and repairs the very constraints that keep its boundary in place. My initial formulation of the criterion, I confess, leaned too heavily on closure alone; it was the vortex counterexample that forced the autonomy axis into the account, and I present the three-axis version precisely because the one-axis version cannot exclude the storm.

This also clarifies how the criterion handles the process-ontological worry raised by Kearney and Rieppel (2022). If organisms are stabilized activities rather than things, then locating their boundary at a surface might seem to reintroduce the thing-like picture the process view rejects. But the informational boundary is not a thing; it is a stable feature of a flow — the surface across which an ongoing activity's information density drops. To individuate by informational closure is to individuate a process by its own dynamics, which is what the process view asks for. The membrane, by contrast, really is a thing, and it is the membrane account, not the informational one, that reifies the organism.

MANY MEMBRANES, ONE INDIVIDUAL: HOLOBIONTS AND COLONIES

The holobiont and the colonial organism share a structure that the membrane account cannot represent: they are single informational individuals distributed across many physical envelopes. In the holobiont, the envelopes belong to different domains of life; in the colony, to genetically near-identical zooids. Yet in both, the composite individuality score peaks at the level of the whole, and the membranes are subordinate parts. The membrane under-counts the self.

Consider the holobiont first. The case for treating host-plus-microbiome as one individual has usually been made in evolutionary terms — whether the ensemble has a shared fate, a hologenome, stable heritable traits (Suárez, 2020; Roughgarden, 2023). Those debates remain unsettled, and Devanesan (2025) is right that the physiological individual and the evolutionary individual can come apart in the holobiont. The informational criterion cuts through part of this by separating the questions. Physiologically, the host and its core microbiome form a tightly integrated information network: microbial metabolites regulate host gene expression, host immune signaling shapes microbial community structure, and the traffic across this interface is denser and more

consequential than the traffic between the ensemble and the external world (Pradeu, 2019). On the informational-closure and autonomy axes, then, the holobiont scores as one individual regardless of how the evolutionary question is settled. What the criterion does not do is collapse the two questions: a system can be a physiological informational individual without being an evolutionary one, and the graded scores make room for exactly that. This is, I think, a virtue rather than an evasion — it locates the disagreement precisely, at the axis where it belongs.

Horizontal gene transfer sharpens the holobiont point in a way worth dwelling on. When heritable information moves across lineage boundaries — as it does extensively among prokaryotes, and as Subotić (2025) documents for extremophilic archaea under simulated extraterrestrial stress — the genetic boundary of the individual becomes porous in exactly the way the informational criterion predicts a boundary can be. The membrane of the donor and recipient cells stays intact; what crosses is information. A membrane-based account has no natural way to register that something individuating has happened, because no membrane was breached in a way that persists. An informational account registers it immediately: the flow of heritable information has redrawn the map of who shares a genetic future with whom. The pangenome concept, discussed in this journal by Markovski (2024), makes the same point at the level of a species: the individual genome is a sample from a larger informational reservoir, not a fixed physical object, and epigenetic carriers extend that reservoir across generations (Souza Mendes, 2024).

The colonial siphonophore makes the "many membranes, one self" structure almost diagrammatic. Nanomia and its relatives are built from zooids that are, developmentally, modified individuals, yet they are specialized as locomotory, feeding and reproductive organs and cannot survive alone; the colony swims, hunts and reproduces as a unit (Sutherland et al., 2019). The coordination required for jet-propelled swimming by multiple nectophores demands inter-zooid signaling of a density that, on the informational-closure axis, unambiguously locates the individual at the colony. Here the membrane account fails in the most visible way: it would have us count each zooid as an organism and the colony as a group, exactly reversing the biology. The active-inference reading of colony-level behavior developed for ant colonies by Friedman, Tschantz, Ramstead, Friston and Constant (2021) generalizes the moral — colonies can be modeled as single inference systems minimizing surprise at the collective level — and the siphonophore is if anything a cleaner case, since its "members" are not even physically separate agents but attached organs.

The two cases together establish the second hypothesis in one of its two directions: informational individuality routinely exceeds membrane individuality, so that many membranes can compose one self. But they also expose a temptation I want to resist. It would be easy to conclude that the fix for the membrane account is simply to "look upward" — to take the informational individual as always larger than the membrane-bounded unit. The syncytium shows why that conclusion is wrong.

ONE MEMBRANE, SEVERAL INDIVIDUALS: THE SYNCYTIAL INVERSION

If holobionts and colonies show individuality exceeding the membrane, the syncytium shows it falling short of the membrane — one continuous envelope containing several partial informational individuals. This is the case that rules out any simple "look one level up" correction and forces a criterion that computes the boundary directly rather than adjusting the membrane by a fixed offset.

A syncytium is a single cell with many nuclei sharing one cytoplasm and one plasma membrane, produced either by nuclear division without cytokinesis or by cell fusion. Naively, the shared membrane and shared cytoplasm suggest a single individual. Recent cell biology

complicates that picture decisively. In the multinucleate fungus studied by Geisterfer, Jalihal, Cole and Gladfelter (2026), messenger RNAs are localized and translated locally, organized by biomolecular condensates, so that the neighborhood around each nucleus can pursue a partly autonomous program of growth and gene expression. The nuclei are not marching in lockstep under a single cytoplasmic dictator; they are semi-independent centers with their own local informational environments. On the integrated-information axis, this means that the whole-cell cause–effect structure is not maximally irreducible — there are internal partitions across which the loss of integrated information is small, which is the formal signature of sub-individuals.

The informational criterion therefore locates more than one individual inside the single membrane, and it does so without embarrassment, because it was never committed to the membrane in the first place. The composite score for the whole syncytium is real but partial; the more informative description is nested, with weak colony-like integration at the whole-cell level and stronger integration within each nuclear domain. This is precisely the structure that shared and nested Markov blankets were introduced to model in the prenatal case by Ciaunica, Levin, Rosas and Friston (2023): a system that is neither cleanly one nor cleanly many, but layered. The syncytium is the sub-cellular analogue of the twin-in-utero, and the same nested formalism applies.

One might object that this proves too much — that if we allow sub-individuals inside a cell, individuality dissolves into an infinite regress of ever-smaller selves. The autonomy axis blocks the regress. A nuclear domain in a syncytium counts as a partial individual only to the extent that it maintains its own constraints; below that scale, at the level of, say, an arbitrary cubic micron of cytoplasm, there is informational structure but no closure of constraints, and so no individual (Bich et al., 2020). The criterion is graded, but it is not unbounded: it finds individuals wherever all three axes are jointly satisfied to some degree, and it finds none where the autonomy axis goes to zero. Where exactly to place the threshold for "counts as an individual" is a decision the criterion exposes rather than hides, and different scientific purposes may set it differently — a point Trappes (2024) makes forcefully about individuality debates generally, and one I am content to concede, because a criterion that makes the threshold explicit is more honest than one that pretends the membrane fixed it for us.

The syncytial inversion has a consequence I did not anticipate when I began and that I think is the most interesting result of the analysis. Because divergence runs in both directions across the three cases, individuality is not merely graded but genuinely scale-relative: the same biological material can be one individual at one scale and several at another, with neither description privileged by the physics. The holobiont is one self that is also billions of microbial selves; the syncytium is several selves that are also one cell; the colony is one animal that is also many zooids. The membrane account, by insisting on a single privileged surface, must declare one of each pair the "real" individual and the other a mere aggregate or mere part. The informational account refuses that forced choice, and in refusing it, matches the biology better. My earlier assumption that a well-posed criterion would return a unique individual per system turned out to be wrong; the better criterion returns a spectrum, and the spectrum is the finding.

CONCLUSION

This article began by asking whether individuality is better located at the physical membrane or at the surface where information flow closes on itself. The three hypotheses that structured the inquiry can now be answered. The first — that a well-defined informational boundary exists for a broad class of biological systems and can be specified without reference to any physical envelope — is supported: the Informational Individuality Criterion assigns coherent three-axis profiles to holobionts, syncytia and colonial organisms using only informational closure,

integrated information and constraint-based autonomy, none of which presupposes a membrane. The second hypothesis — that the informational boundary diverges from the membrane in both directions — is confirmed and, in my view, is the central empirical yield of the analysis: membranes under-count the self in the holobiont and the colony and over-count it in the syncytium, so that no fixed correction to the membrane could recover the informational individual. The third hypothesis — that individuality so defined is graded and often nested — is likewise supported, and in a stronger form than I initially expected: divergence in both directions makes individuality scale-relative, so that the same material can carry individuals at more than one scale at once.

The principal original contribution of this article is the Informational Individuality Criterion itself: a three-axis, scorable operationalization that locates the organismal boundary at the surface of maximal informational closure and diagnoses, through the membrane–information divergence classification, how far and in which direction that boundary departs from the physical membrane. The contribution is not another verbal definition of the individual but an instrument that binds three previously separate formal traditions — the information theory of individuality, integrated information, and organizational autonomy — into a single procedure and tests it against the cases those traditions have tended to discuss in isolation. Where prior accounts argued about which criterion is correct, the IIC lets one score a system on all three axes and read off the answer, including the answer that a system is several individuals at once. That, I think, is progress of a modest but usable kind.

The limitations are real and I state them without softening. First and most serious is the single-coder design: I assigned every axis value myself from the literature, without independent raters, so the composite scores carry an unquantified subjectivity that inter-rater reliability testing would expose and, I expect, partly correct. Second, the axis measures are operationalized informally here; a fully computed criterion would require estimating mutual-information partitions, system-level integrated information, and constraint closure from actual data, each of which is technically demanding and, for integrated information in particular, computationally severe at biological scale. Third, my three test systems were chosen precisely because they break the membrane intuition, which means they are a biased sample; the criterion's behavior on ordinary, membrane-coincident organisms is trivial by construction and tells us little. Fourth, I have leaned on the free-energy and Markov-blanket literature for the closure axis while also endorsing a serious critique of that literature (Bruineberg et al., 2022), and although I have tried to take only the weaker, defensible commitment, a reader who rejects the framework wholesale will discount the first axis accordingly.

Three directions for future work follow. The first is empirical operationalization: computing, rather than estimating, the three axes for a real holobiont or syncytium using time-series data, which would turn the heuristic into a measurement. The second is the threshold problem: making principled, purpose-relative decisions about how high the composite score must be for a system to "count" as an individual, rather than leaving the threshold implicit. The third is evolutionary: asking whether transitions in individuality (Doulcier et al., 2023; Bourrat, 2019) are, at bottom, transitions in informational closure — whether the major transitions can be redescribed as events in which a new informational boundary formed and stabilized above an older one. That last question I cannot settle here, but if the informational criterion is right, then the history of individuality is the history of information learning to close on itself at ever-higher scales, and the membrane, for all its ancient importance, was never where the self really lived.

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INFORMACIONA TEORIJA BIOLOŠKE INDIVIDUALNOSTI: KAKO GRANICE ORGANIZMA NASTAJU IZ PROTOKA INFORMACIJA, A NE IZ FIZIČKIH MEMBRANA

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Sažetak: Gdje prestaje jedan organizam a počinje njegova okolina? Uobičajeni odgovor u biologiji je prostoran: granica je spoljašnja membrana, koža, ćelijski zid. Ovaj rad tvrdi da je membrana loš vodič individualnosti i da se granica organizma bolje smješta tamo gdje se protok informacija zatvara sam u sebe. Razvijam Kriterijum informacione individualnosti (IIC), operacionalizaciju na tri ose koja ocjenjuje svaki kandidat-sistem duž informacione zatvorenosti (odnos unutrašnje prediktivne uzajamne informacije prema onoj koja prelazi granicu), integrisane informacije (nesvodivost uzročno-posljedične strukture sistema) i autonomije zasnovane na ograničenjima (organizaciona zatvorenost ograničenja koja održavaju sistem). Prema ovom pristupu, granica organizma je zatvorena površina koja maksimizuje kompozitni funkcional individualnosti, a ne površina koju crta lipidni dvosloj. Kriterijum provjeravam na tri slučaja koji ruše membransku intuiciju u suprotnim smjerovima: sisarski holobiont, u kojem mnoge membrane zatvaraju jednu informacionu jedinku; višejedarni sincicij, u kojem jedna membrana zatvara nekoliko djelimično autonomnih informacionih podjedinki; i kolonijalni sifonofor, u kojem su mnoge membrane zooida podređene jednoj integrisanoj kolonijalnoj jedinki. U sva tri slučaja informaciona granica sistemski odstupa od fizičke membrane, a taj razmak kvantifikujem dijagnostikom membransko-informacione divergencije. Zaključak je da je individualnost stepenovana, ponekad ugnježđena i često pomjerena sa membrane — ishod koji membranski kriterijumi ne mogu prikazati, a koji informacioni kriterijum čini preciznim i, u načelu, mjerljivim.

Ključne riječi: *biološka individualnost, protok informacija, integrisana informacija, kauzalna zatvorenost, autonomija, holobiont, sincicij, kolonijalni organizmi.*