PSE Research Programme

# Biological Individuality

*The Principle of Systematic Exclusion as a Relational Theory of Biological Individuality*

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## PSE Monographs (Series Statement)

The PSE Monograph Series develops the theoretical, conceptual, and empirical foundations of the PSE Research Programme.

The programme investigates whether organization can be understood as a primary ontological category and whether the emergence, persistence, and transformation of organized systems can be explained through a common generative principle operating across multiple domains of reality.

Each monograph addresses a distinct scientific question while contributing to a cumulative investigation of organization across physical, biological, cognitive, symbolic, institutional, technological, and social systems.

Together, the series develops a unified conceptual framework without reducing domain-specific theories to a single explanatory model. Established scientific disciplines retain their explanatory autonomy while being interpreted as complementary investigations of different realizations of organized reality.

Following the ontological foundations established in Ontology of Organization (Monograph No. 2), this volume investigates one of biology's central conceptual problems: biological individuality. It examines whether the diverse concepts of individuality developed in contemporary biology can be understood as complementary manifestations of a common organizational architecture and how that architecture relates to the Principle of Systematic Exclusion.

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# Biological Individuality

***The Principle of Systematic Exclusion as a Relational Theory of Biological Individuality***

## Preface

This monograph is the third volume in the PSE Research Programme and the first to examine the organizational framework developed in the preceding monographs within a specifically biological problem.

Monograph No. 1 established the architecture, methodological commitments, and research strategy of the programme. Monograph No. 1A defined its canonical terminology and conceptual dependencies. Monograph No. 2 developed the domain-independent ontology of organization on which the present investigation builds.

Biological individuality provides a demanding next step. Biology offers no single, uncontested criterion by which an individual can always be identified. Anatomical boundaries, physiological integration, developmental continuity, ecological relations, and evolutionary continuity may converge in familiar organisms while diverging in symbiotic associations, microbial collectives, and social systems.

The purpose of this monograph is to investigate whether these differences can be examined within a common organizational framework without reducing them to a single biological criterion.
Living cells, biofilms, holobionts, and eusocial insect colonies are compared across six dimensions of biological organization: Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity.

The analysis represents a further step in testing the explanatory scope of the PSE framework. Concepts developed at a domain-independent level must acquire empirical significance through confrontation with the theories, mechanisms, and distinctions of established scientific disciplines.
Biology is treated here neither as an illustration of PSE nor as a domain to which a completed ontology is simply applied. It provides an independent field in which the proposed organizational architecture can be examined, constrained, and, where necessary, revised.

The resulting account remains deliberately open. Biological Individuality is investigated as a relational problem, and Organizational Scale Invariance as a research hypothesis. Their scientific value will depend upon whether the framework clarifies existing biological problems, supports informative comparisons, and ultimately generates propositions capable of independent empirical examination.

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2026

## Abstract

Biological individuality is expressed through multiple and partly independent dimensions, including organizational boundaries, integration, adaptive persistence, developmental continuity, ecological coupling, and evolutionary continuity. No single biological criterion adequately captures this diversity. This monograph develops a relational account of biological individuality from the ontological framework of the Principle of Systematic Exclusion (PSE). It begins from the domain-independent concepts of Persistent Organization and Organizational Identity developed within the PSE Research Programme and examines how these acquire specifically biological form.
Four contrasting cases are analyzed: living cells, biofilms, holobionts, and eusocial insect colonies. Each is evaluated across six dimensions of biological organization.

The comparison shows that biological individuality is neither exhausted by organismal boundaries nor reducible to genetic, physiological, developmental, ecological, or evolutionary criteria considered separately. Instead, biological individuality is investigated relationally through the organizational dimensions by which a distinguishable biological organization maintains continuity through time and within a specific Context.

The analysis further identifies recurrent organizational relations across markedly different biological scales. This provides a basis for formulating *Organizational Scale Invariance* as a PSE research hypothesis: comparable organizational architecture may recur across scales while being realized through different domain-specific mechanisms.
The comparative cases support the plausibility of this hypothesis without establishing it as a general biological law.

Biological individuality is treated as graded, multidimensional, and context-dependent. The resulting framework integrates established approaches to individuality without replacing their domain-specific explanatory contributions and provides a common organizational basis for further comparative and empirical investigation.

**Keywords:** biological individuality; Principle of Systematic Exclusion (PSE); biological organization; persistent organization; organizational identity; organizational boundaries; organizational integration; adaptive persistence; ecological coupling; organizational scale invariance

# Part I — The Biological Problem

## Chapter 1 — The Problem of Biological Individuality

### 1.1 Why Biological Individuality?

Few concepts in biology appear as self-evident as that of the biological individual. Organisms are counted, classified, observed, and compared. They develop, reproduce, interact, and evolve. The individual organism has served as one of biology's most familiar units of observation and explanation.

Closer examination reveals a more difficult problem. Contemporary biology encounters living systems whose anatomical, physiological, developmental, ecological, and evolutionary boundaries do not necessarily coincide. Symbiotic associations connect organisms with different evolutionary histories; microbial collectives can display coordinated organization; and highly integrated biological systems may consist of components that retain substantial organizational independence.

Such cases complicate the assumption that biological individuality can be identified through a single defining property. Anatomical separation, physiological integration, developmental continuity, reproduction, evolutionary interests, and ecological dependence can each provide biologically significant indications of individuality, yet they may identify different boundaries or different levels of organization.
Biological individuality therefore presents a fundamental question:

> *what warrants treating a living organization as an individual when the different forms of biological continuity do not necessarily coincide?*

This question provides the point of departure for the present monograph.

### 1.2 The Limits of the Classical Organism Concept

The classical concept of the biological individual is closely associated with the discrete organism: an anatomically distinguishable living system displaying physiological integration, developmental continuity, and reproductive organization.
This conception remains biologically informative and provides an effective description of many familiar organisms. Its limitations become apparent when these characteristics no longer identify the same biological boundary or organizational level.

Contemporary approaches emphasize different aspects of individuality. Evolutionary accounts examine participation in Darwinian processes and the levels at which selection operates. Physiological and immunological approaches investigate functional integration and the regulation of biological integrity. Developmental perspectives emphasize continuity through biological change, while ecological and relational approaches examine the interactions through which living systems persist in relation to their environments.

These perspectives need not represent competing definitions of the same property. They address different biological processes and can therefore identify different aspects or levels of individuality.
Their partial divergence reflects a substantive feature of the biological problem: anatomical, physiological, developmental, ecological, and evolutionary forms of continuity do not necessarily coincide.

The limitation of the classical organism concept lies in its inability to provide a universally applicable criterion of biological individuality. The resulting plurality raises the question that guides the analysis developed in this monograph:

> *Do contemporary concepts of biological individuality describe fundamentally different forms of individuality, or do they identify different dimensions of biological organization whose relations can be investigated comparatively?*

## 1.3 From Organism to Organization

The difficulties surrounding biological individuality suggest a shift in analytical emphasis. Instead of beginning with the assumption that the biological individual must coincide with a discrete organism, the analysis can begin with biological organization and ask how identifiable living systems maintain continuity through change.

This shift directs attention from material composition alone to the relations and processes through which biological organization persists. Living systems continuously exchange matter and energy, replace components, interact with surrounding organisms and environments, and undergo developmental change. Their continuity therefore cannot generally be understood as the continued presence of the same material constituents.

*Organization* provides a different point of entry. It allows the analysis to examine how boundaries are maintained, processes are integrated, viable organization persists under changing conditions, developmental states remain connected, ecological relations contribute to continuity, and evolutionary continuity is established across generations. These forms of continuity need not coincide at the same organizational level.

The resulting question is more specific than whether a biological system persists. It concerns under which biological conditions persistent organizational identity can justifiably be attributed to a biological individual.

This formulation preserves a distinction that will remain central throughout the monograph. *Persistent Organization* concerns the continuation of identifiable organization through change. Biological Individuality concerns the biological interpretation of such continuity and requires additional analysis of the organizational relations through which it is realized.

### 1.4 Scope and Objectives

This monograph develops an integrative organizational framework for comparing existing theories of biological individuality while preserving their distinct explanatory domains. Contemporary biology reveals a substantial diversity of organizational forms, making it unlikely that biological individuality can be captured adequately by a single defining criterion. Existing concepts are examined as potentially complementary accounts of different dimensions of biological organization.

The PSE framework provides the ontological point of departure for investigating whether these dimensions can be related through a common organizational architecture while retaining the empirical specificity and explanatory contributions of established biological theories (Stolting, 2026a).

The argument proceeds in four stages. Chapter 2 reviews principal concepts of biological individuality in contemporary biology and philosophy of biology. Chapters 3 and 4 develop the organizational framework from the foundations established in Monograph No. 2. Chapters 5 through 8 apply this framework to contrasting forms of biological organization, after which Chapter 9 compares the resulting organizational profiles. Chapter 10 evaluates what these comparisons imply for a relational account of biological individuality and for the broader PSE Research Programme.

The objective is to determine whether biological individuality can be analyzed more precisely by distinguishing the domain-independent conditions of Persistent Organization and Organizational Identity from the additional biological dimensions through which individuality is constituted.

The analysis does not assume in advance that these dimensions converge upon a universal criterion, nor that every form of persistent biological organization constitutes a biological individual.

## Chapter 2 — Existing Concepts of Biological Individuality

### 2.1 Introduction

Biological individuality has become a major conceptual problem because the properties commonly associated with individual organisms do not always identify the same biological entity. Anatomical boundaries, physiological integration, developmental continuity, ecological relations, reproduction, and participation in evolutionary processes may coincide in familiar organisms while diverging in other forms of biological organization.

Contemporary approaches emphasize different aspects of individuality. Evolutionary accounts examine the entities that participate in Darwinian processes. Physiological and immunological approaches focus on functional integration and the maintenance of biological integrity. Developmental approaches emphasize continuity through biological change, while ecological

and relational perspectives examine the interactions through which living systems persist in relation to other organisms and their environments.
Process-oriented approaches further question whether individuality should be understood primarily as a property of bounded entities or as continuity maintained through ongoing organization.

These approaches need not provide mutually exclusive definitions. Each addresses biologically significant relations and processes, yet they may identify different boundaries, different forms of continuity, or different organizational levels.
Their plurality therefore raises a comparative question: *how are these different dimensions of biological individuality related?*

This chapter reviews the principal approaches relevant to that question. Its purpose is not to select a preferred definition in advance, but to establish the conceptual field within which a more general organizational analysis can subsequently be developed.

## 2.2 Classical Individuality

A familiar conception of biological individuality identifies the individual with the discrete organism. Organisms can often be distinguished through recognizable anatomical boundaries, coordinated physiological processes, integrated development, and reproductive continuity. These characteristics frequently coincide and together provide an effective basis for identifying many plants and animals as biological individuals.

Within this conception, individuality is closely associated with morphological integrity and functional integration. Cells, tissues, and organs participate in the organization of a larger living system, while the organism maintains a recognizable continuity despite continuous material and physiological change.

The limitations of this conception become apparent when its characteristic forms of continuity no longer coincide. Anatomical boundaries may be permeable, physiological functions may depend upon symbiotic partners, developmental processes may involve interactions among genetically distinct organisms, and reproductive or evolutionary continuity may be organized at levels that do not correspond straightforwardly to the anatomically bounded organism.

The classical organism concept remains an important biological reference point. Its limitation lies in its inability to provide a universally applicable criterion of individuality when different forms of biological continuity identify different boundaries or organizational levels.

## 2.3 Evolutionary Individuality

Evolutionary approaches to biological individuality focus on the role that biological entities play in Darwinian processes. A central question is which entities participate as individuals in processes involving variation, heredity, reproduction, and differential reproductive success, and at which organizational levels these processes occur.

From this perspective, the evolutionary individual need not coincide with the anatomically bounded organism.
Cells, multicellular organisms, colonies, social groups, and symbiotic associations can constitute relevant units of evolutionary analysis under particular conditions. Which entities qualify as evolutionary individuals consequently depends upon how variation, heredity, reproduction, and differential fitness are organized at the relevant level.

Godfrey-Smith (2009) analyzes evolutionary individuality through the structure of Darwinian populations, in which properties such as variation, heredity, and differences in reproductive success can occur to different degrees. Queller and Strassmann (2009) approach organismality through the balance between cooperation and conflict among constituent parts.
Both approaches allow biological individuality to vary in degree, although the dimensions along which that variation is characterized differ.

Evolutionary individuality may identify organizational levels that do not coincide with those identified by physiological or developmental criteria. A system displaying substantial physiological integration need not thereby constitute an evolutionary individual, while entities relevant to evolutionary processes need not exhibit the degree or form of physiological integration associated with the classical organism.

Evolutionary approaches identify a distinct dimension of the individuality problem. They provide criteria for investigating how biological entities participate in evolutionary processes while leaving open how evolutionary individuality relates to other forms of biological continuity and integration.

## 2.4 Physiological and Immunological Individuality

Physiological approaches to biological individuality emphasize the functional integration through which living systems maintain their organization. Metabolic processes, regulatory mechanisms, and coordinated interactions among biological components contribute to the continued functioning of the system despite ongoing material exchange and internal change.

From this perspective, individuality is associated with the organization of processes that maintain biological integrity *through time*. The relevant boundary need not function as an impermeable separation from the environment. Living systems depend upon continuous exchanges of matter and energy, making regulated interaction with their surroundings integral to their physiological organization.

Immunological approaches add another dimension by examining how biological systems regulate interactions among endogenous and exogenous elements. Earlier conceptions often emphasized discrimination between self and non-self, whereas subsequent approaches have focused increasingly on processes of tolerance, regulation, and the maintenance of biological continuity.
Pradeu (2012), for example, develops an account in which immunological individuality depends upon the continuity of interactions between immune components and the biological elements with which they interact, without requiring an absolute separation between self and non-self.

These questions become particularly significant in organisms that maintain persistent associations with microbial communities. Microorganisms may contribute to physiological processes while remaining biologically distinct entities with their own organizational and evolutionary histories. Physiological integration can therefore extend across relations whose status with respect to biological individuality remains open.

Physiological and immunological approaches identify forms of integration and regulation that cannot be inferred from evolutionary individuality alone. They direct attention to the processes through which biological integrity is maintained while leaving open whether physiological, immunological, and evolutionary boundaries coincide in a particular biological system.

## 2.5 Developmental and Process Individuality

Developmental approaches introduce a temporal dimension into biological individuality. Living systems undergo growth, differentiation, renewal, and other forms of transformation while retaining forms of continuity through successive biological states.
Individuality can therefore be investigated through the developmental relations connecting these states over time.

This perspective shifts attention from the properties of a biological system at a particular moment to the continuity of its developmental history. Substantial structural and functional change can occur without necessarily interrupting that history, while reproduction or the formation of successor systems raises a different question concerning the relation between developmental continuity and continuity across generations.

Process-oriented approaches extend this temporal perspective by treating living systems as dynamically maintained organizations. Cells divide, tissues are renewed, physiological states change, and relations with the environment are continually reorganized.
Nicholson and Dupré (2018) develop this perspective within a broader processual philosophy of biology, in which organisms are understood as processes whose relative stability depends upon continuing biological activity and organization.

Developmental and process approaches emphasize continuity through transformation rather than the persistence of an unchanged biological state.
They also raise an important question for biological individuality:

> *which changes belong to the continuing history of the same biological organization, and which mark reproduction, succession, or the emergence of a different organization?*

This temporal distinction becomes especially important when developmental continuity, individual persistence, and evolutionary lineage continuity do not coincide at the same organizational level.

## 2.6 Ecological and Relational Individuality

Ecological and relational approaches extend the analysis of biological individuality beyond processes occurring within anatomically bounded organisms. Living systems persist through interactions with other organisms and with environmental conditions that contribute to their metabolism, development, regulation, and continued viability.
Some of these relations are transient, whereas others become recurrent or constitutive features of biological organization.

Symbiotic associations make this problem particularly visible. Organisms belonging to different evolutionary lineages can participate in persistent biological relations in which their physiological or developmental processes become closely interconnected. Such integration complicates any straightforward identification of biological individuality with anatomical separation or common evolutionary descent.

The holobiont concept provides an important example. A host and its associated microorganisms can form a biologically consequential relational system, yet the existence of such relations does not by itself establish that the resulting association constitutes a biological individual. Its components may differ in persistence, transmission, reproductive continuity, and evolutionary interests, and the organizational boundaries relevant to one biological process may therefore differ from those relevant to another (Bordenstein & Theis, 2015; Gilbert et al., 2012; McFall-Ngai et al., 2013).

Relational approaches require a distinction between participation in an ecological network and relations that are constitutive of the organization whose individuality is under investigation. Dependence, interaction, or mutual influence alone cannot determine where biological individuality should be located.

Ecological and relational individuality introduces Context, *in the canonical PSE sense*, as an integral part of the problem (Stolting, 2026b).
The question is not only how a living system is internally organized, but which organism–organism and organism–environment relations contribute to the continuity of that organization, and whether those relations justify extending the attribution of individuality beyond the boundaries of a conventionally defined organism.

## 2.7 Pluralistic Approaches

The diversity of criteria associated with biological individuality has encouraged pluralistic approaches in which different concepts of individuality are applied to different biological questions. Anatomical, physiological, developmental, ecological, and evolutionary criteria may each identify biologically significant forms of continuity without necessarily identifying the same entity or organizational level.

Such pluralism has an important methodological advantage. It allows concepts of individuality to remain responsive to the processes under investigation instead of requiring all biological phenomena to conform to a single universal criterion.

An entity relevant as an evolutionary individual, for example, need not possess the same boundaries or form of integration as an entity identified through physiological or developmental criteria.

Pluralism, however, leaves a further question unresolved. If different criteria identify different aspects or levels of biological organization, their relations still require explanation. The observation that several concepts of individuality can be scientifically legitimate does not establish whether the organizational properties they identify are independent, complementary, overlapping, or hierarchically related.

The resulting problem is comparative as well as definitional.

> *When different criteria of biological individuality identify different entities or organizational levels, what relations exist among the forms of organization on which those attributions are based?*

This question provides the basis for the comparative synthesis developed in the following section.

## 2.8 Comparative Synthesis

The approaches reviewed in this chapter show that biological individuality can be investigated through different biological processes and relations. Evolutionary participation, physiological and immunological integration, developmental continuity, ecological relations, and the boundaries associated with these processes need not identify the same entity or organizational level.

This divergence is biologically significant. It indicates that disagreement about individuality cannot always be resolved by selecting one criterion over another, since different criteria may address different forms of biological organization.

At the same time, recognizing this plurality does not explain how the organizational properties identified by these approaches are related. The resulting problem is one of comparative organization.

- Which organizational relations recur across different accounts of biological individuality?
- Which remain specific to particular biological processes or levels?
- And under which organizational and contextual conditions does the attribution of individuality to a biological organization become warranted?

Addressing these questions requires a conceptual basis that does not already presuppose biological individuality. Chapter 3 therefore begins from the more general concepts of Persistent Organization and Organizational Identity developed in Ontology of Organization (Monograph No. 2).
Because these concepts apply beyond biology, they cannot by themselves establish biological individuality. They provide the domain-independent point of departure from which the additional organizational characteristics relevant to living systems can be investigated.

Chapter 4 develops the comparative dimensions used for that investigation. The subsequent case studies then examine how these dimensions occur and combine in different forms of biological organization, without assuming in advance that they must converge upon a single criterion or organizational level of individuality.

# Part II – From Organization to Biological Individuality

## Chapter 3 – The Ontological Foundation

### 3.1 The Ontological Point of Departure

Ontology of Organization (Monograph No. 2; Stolting, 2026c) developed a domain-independent organizational architecture based upon the Principle of Systematic Exclusion (PSE). Within this architecture, organization arises in Context through conceptually dependent stages of Distinction, Systematic Exclusion, Boundary, Constraint, Selective Persistence, Coherence, Persistent Organization, and Identity.
The sequence specifies proposed organizational dependencies without prescribing the domain-specific mechanisms through which they are realized.

Biological organization provides a distinct domain in which this architecture can be examined. Its application to living systems requires biological analysis because the domain-independent concepts of Persistent Organization and Organizational Identity do not by themselves establish biological individuality.

The question addressed here is more specific:

> *under which biological conditions can persistent organizational identity constitute biological individuality?*

The organizational architecture inherited from Monograph No. 2 provides the ontological point of departure for this investigation. Its adequacy for biological individuality remains to be established through comparison with biological concepts and cases.
The analysis must therefore determine which additional characteristics of living organization are relevant to the attribution of individuality and how they relate across different biological systems.

The following sections develop the conceptual basis for that comparison, beginning with Persistent Organization and Organizational Identity before examining their application to biological organization.

### 3.2 Persistent Organization

Persistent Organization refers to the continued maintenance of an organization through time despite changes in its components, states, or relations. Persistence therefore concerns continuity of organization, not the permanence of the material elements through which that organization is realized.

Within the PSE architecture, persistence depends upon selective relations between an organization and its Context. Boundaries and constraints regulate which interactions and transformations remain compatible with continued organization. Selective Persistence refers to the resulting differential continuation of organizational configurations: configurations

compatible with the conditions of persistence can continue, whereas incompatible configurations cannot be maintained as the same organization.

Persistent Organization emerges when such selective relations sustain sufficient Coherence for an organization to continue through change. Coherence concerns the compatibility of relations within the organization. It does not by itself establish Congruence with Context, nor does persistence imply that an organization is adaptive, living, or individual. These terms retain their canonical PSE meanings (Stolting, 2026b).

Persistent Organization is a domain-independent ontological concept. Physical, biological, technological, or other organized systems may display persistence without thereby possessing the characteristics associated with biological organization or biological individuality.

This distinction is essential for the present analysis. Biological individuality cannot be inferred from persistence alone. Persistent Organization provides the more general organizational basis from which Organizational Identity can be considered before the additional characteristics of biological organization are examined.

### 3.3 Organizational Identity

Persistent Organization provides the basis for Organizational Identity: the continuity through which an organized system remains identifiable across successive states despite structural, material, or relational change.
Organizational Identity is used here in this systems-theoretical sense and should not be conflated with the philosophical problem of strict numerical identity.

The distinction between persistence and identity is conceptually important. Persistence concerns the continuation of organization through time. Organizational Identity concerns the continuity by which successive organizational states can be related as states in the history of the same organized system.
Organizational Identity depends upon sufficient continuity in the organizational relations through which that system persists.

Organizational Identity does not require structural invariance. Components may be replaced, relations reorganized, and system states transformed while sufficient organizational continuity is maintained for the organization to remain identifiable through those changes.
What constitutes sufficient continuity depends upon the organization and Context under investigation and cannot be determined from material continuity alone.

Like Persistent Organization, Organizational Identity is domain-independent. Physical, biological, ecological, technological, and social organizations may retain recognizable identity through change. Organizational Identity therefore cannot by itself distinguish a biological individual from other forms of persistent organization.

This establishes the next step in the analysis:

> *which characteristics of living organization are relevant when Organizational Identity is considered in the biological domain?*

## 3.4 Biological Organization

Living systems can be distinguished from persistent organization in general by the processes through which their continued organization is maintained. Metabolism, regulation, repair, development, and selective interaction with environmental conditions contribute to the ongoing maintenance and transformation of living organization under conditions of material turnover and environmental change.

Several established theoretical frameworks address aspects of this organization. Autopoietic theory emphasizes the self-production and organizational closure of living systems (Maturana & Varela, 1980). Accounts of biological autonomy examine networks of mutually dependent constraints through which living systems contribute to maintaining the conditions of their own existence (Moreno & Mossio, 2015). Evolutionary approaches investigate reproduction, heredity, variation, and differential reproductive success at different organizational levels (Godfrey-Smith, 2009). Ecological approaches emphasize the organism–environment relations upon which biological persistence depends (Nicholson & Dupré, 2018).

These perspectives address different processes and need not define biological organization in identical terms. They nevertheless show why biological persistence requires domain-specific analysis. Living systems maintain organizational continuity through regulated processes while remaining materially and functionally dependent upon relations with their Context.

Biological Organization is therefore treated here as a domain-specific realization of Persistent Organization characterized by the active maintenance and regulation of living processes in relation to Context.

This formulation does not by itself establish biological individuality. Nor does it imply that every process associated with living organization must occur within the same boundary or at the same organizational level.

The relevant question is which characteristics of Biological Organization contribute to the attribution of Biological Individuality, how those characteristics relate to one another, and whether they converge or diverge across different living systems.
Chapter 4 develops the comparative dimensions through which that question will be investigated.

## 3.5 From Organizational Identity to Biological Individuality

The preceding analysis establishes a hierarchy of conceptual specification. Persistent Organization provides a domain-independent basis for organizational continuity; Organizational Identity concerns the continuity through which successive states can be related to the same organized system; and Biological Organization specifies the active maintenance and regulation characteristic of living systems.

Biological Individuality introduces a further question. The presence of Biological Organization does not determine by itself whether a living system should be regarded as an individual,

because the processes contributing to its persistence may occur across different boundaries and organizational levels. Physiological integration, developmental continuity, ecological dependence, and evolutionary continuity may converge in some living systems while diverging in others.

Biological Individuality is investigated here as a possible attribution to living organizations through the relations among relevant forms of biological continuity and integration. Whether particular organizational configurations warrant that attribution must be examined comparatively across biologically different forms of organization.

Chapter 4 develops a set of analytical dimensions for this comparison. These dimensions are not proposed as necessary or sufficient criteria of Biological Individuality. They provide a common framework for examining how different forms of biological continuity and integration combine, diverge, and occur at different organizational levels.

### 3.6 Orientation for the Comparative Analysis

The transition from ontology to biological comparison also marks a transition in method. The domain-independent architecture introduced in the preceding sections provides the conceptual point of departure; the following chapters examine its analytical value across biologically different forms of organization.

Chapter 4 develops a common set of organizational dimensions for this comparison. These dimensions are derived from biological processes and relations identified in the literature reviewed in Chapter 2 and are used as analytical variables rather than as predefined criteria of Biological Individuality.

Chapters 5 through 8 apply the same dimensions to living cells, biofilms, holobionts, and eusocial insect colonies.
Using a common analytical framework makes it possible to compare how organizational relations combine, diverge, and occur at different levels without presupposing that the cases represent successive degrees of individuality.

Chapter 9 compares the resulting organizational profiles. The purpose of that comparison is to determine what the framework clarifies, where its explanatory limits become apparent, and whether recurring organizational relations can be identified independently of the dimensions through which the cases were initially described.

The comparative analysis evaluates both the biological problem of individuality and the explanatory contribution of the proposed organizational framework. Its value depends upon whether it reveals relations that are not already captured by the established concepts reviewed in Chapter 2.

# Chapter 4 — Dimensions of Biological Organization

## 4.1 Beyond Persistent Organization

Persistent Organization and Organizational Identity provide the domain-independent basis for the analysis developed in Chapter 3. Biological individuality, however, requires comparison of the specifically biological processes and relations through which living organization is maintained across time and in relation to Context.

The literature reviewed in Chapter 2 indicates that these processes do not necessarily identify the same boundary or organizational level. Physiological integration may occur across relations that differ from those relevant to evolutionary continuity; developmental continuity need not coincide with reproductive succession; and ecological dependence may extend beyond the organization whose individuality is under consideration.
A comparative framework must therefore preserve these differences while allowing their organizational relations to be examined systematically.

Six dimensions are used for this purpose:

1. Organizational Boundaries — the relations through which an organization is distinguished from and selectively connected with its Context;
2. Organizational Integration — the coordination and interdependence among processes contributing to continued organization;
3. Adaptive Persistence — the capacity to maintain viable organizational continuity under changing conditions;
4. Developmental Continuity — continuity of organization across developmental transformation;
5. Ecological Coupling — the organism–organism and organism–environment relations relevant to continued organization;
6. Evolutionary Continuity — continuity associated with reproduction, heredity, variation, and evolutionary processes across generations.

These dimensions are analytical variables, not necessary or sufficient criteria of Biological Individuality. Their presence does not imply that they coincide at the same boundary, operate at the same organizational level, or contribute equally to individuality in every biological system.

The purpose of the framework is *comparative*. By applying the same dimensions across different forms of biological organization, the analysis can examine where they converge, where they diverge, and how their relations bear upon the attribution of Biological Individuality.

## 4.2 Organizational Boundaries

Boundary is a domain-independent concept within the PSE architecture (Stolting, 2026b). It refers to the organizational distinction through which a persistent organization remains distinguishable from its Context and through which interactions relevant to its continuation become selectively constrained.
A boundary therefore need not coincide with a physical enclosure.

In biological systems, such organizational distinctions are realized through diverse mechanisms and relations. Cellular membranes regulate molecular exchange; epithelial tissues organize interfaces between physiological compartments and external conditions; immune processes contribute to the regulation of interactions among endogenous and exogenous elements; and collective biological systems may maintain distinguishability through spatial, behavioral, chemical, or ecological relations (Alberts et al., 2022; Pradeu, 2012).

Organizational Boundaries designates this biological dimension: the processes and relations through which a living organization remains distinguishable from its surroundings while regulating interactions relevant to its continuation.
Such boundaries can be materially localized, distributed across several structures or processes, or dynamically maintained through continuing interaction.

Boundary organization must be distinguished from simple spatial separation. A biological system can remain materially open while maintaining selective relations that contribute to its organizational continuity. Conversely, physical proximity or enclosure alone does not establish that the enclosed components participate in the same biological organization.

The comparative question is not whether a biological system possesses a boundary in the abstract, but how its organizational boundaries are realized, which interactions they regulate, at which organizational level they operate, and whether those boundaries coincide with the other dimensions relevant to Biological Individuality.

### 4.3 Organizational Integration

Organizational Boundaries concern the relations through which a biological organization remains distinguishable from and selectively connected with its Context. A second dimension concerns the coordination and interdependence of the biological processes through which that organization is maintained.

Organizational Integration refers to the coordination and interdependence of biological processes or components contributing to the continuation of an organization. Metabolic pathways, regulatory networks, developmental processes, physiological coordination, and behavioral interactions can each contribute to integration, depending upon the biological system and organizational level under investigation.

Organizational Integration is analytically distinct from Coherence as canonically defined within the PSE framework (Stolting, 2026b).
Coherence is the domain-independent compatibility of relations within persistent organization. Organizational Integration concerns the biologically realized coordination and interdependence through which processes or components contribute to continued living organization. Integration may therefore provide a domain-specific realization relevant to Coherence without being identical to it.

Integration does not require uniformity or the loss of organizational independence among participating components. Biological entities with distinct boundaries, developmental histories, or evolutionary interests may participate in coordinated relations that contribute to organization

at another level. The existence of such coordination does not by itself establish Biological Individuality at that level.

Organizational Integration is examined comparatively through the mechanisms and relations by which biological processes become coordinated, the organizational level at which that coordination occurs, and its contribution to continued organization. Its significance for Biological Individuality depends upon how it relates to the other dimensions rather than upon integration alone.

### 4.4 Adaptive Persistence

Biological organizations persist under conditions that continually change. Environmental fluctuations, resource availability, disturbance, physiological stress, and changes within the organization itself can alter the conditions under which continued living organization remains possible.
Biological persistence therefore involves more than the continuation of an unchanged organizational state.

Adaptive Persistence refers here to the capacity of a biological organization to maintain viable organizational continuity under changing conditions. Such continuity may involve regulation, physiological adjustment, behavioral change, repair, reorganization, or other responses through which living processes remain compatible with continued organization.

Adaptive Persistence is analytically distinct from Persistence in the domain-independent PSE architecture. Persistence concerns the continuation of organization through time. Adaptive Persistence concerns the capacity of living organization to maintain that continuity when relevant conditions change. It may therefore require organizational change rather than preservation of a previous state.

Adaptive Persistence must also be distinguished from evolutionary adaptation. Evolutionary adaptation concerns changes in populations or lineages through evolutionary processes across generations. Adaptive Persistence, as used here, concerns the continued viability of biological organization under changing conditions and can occur through processes operating within the lifetime or organizational history of the system under investigation. Evolutionary change may contribute to persistence across generations, but it is not presupposed by this dimension.

The comparative analysis examines how biological systems respond to changing conditions, which organizational processes contribute to continued viability, and at which organizational level those responses occur.
The presence of such responses does not by itself establish Biological Individuality; their significance depends upon how Adaptive Persistence relates to the other organizational dimensions.

## 4.5 Developmental Continuity

Biological organizations can undergo substantial transformation while maintaining continuity through successive stages of their organizational history. Growth, differentiation, structural reorganization, and changes in physiological organization may alter the state of a living system without necessarily interrupting the continuity through which that system develops.

Developmental Continuity refers to the continuity of biological organization across such developmental transformation. It concerns the relations through which successive developmental states remain connected within the organizational history of the system under investigation.

Developmental Continuity must be distinguished from the persistence of an unchanged state. Development itself may involve extensive organizational transformation. The relevant question is whether these transformations remain connected through processes that sustain continuity across successive developmental states.

Developmental Continuity must also be distinguished from reproductive succession and evolutionary lineage continuity. Reproduction may generate a new biological organization whose history is causally and developmentally related to that of another organization without constituting the continued persistence of the same individual organization. Similarly, continuity across generations can be evolutionarily significant without implying continuity of the same Biological Individual.

The comparative analysis examines how developmental states are connected through time, which organizational processes maintain that continuity, where discontinuities or reproductive transitions occur, and at which organizational level developmental continuity can be identified. Its significance for Biological Individuality depends upon its relation to the other organizational dimensions.

## 4.6 Ecological Coupling

Biological organizations persist through continuing relations with other organisms and with their environments. These relations provide resources, impose constraints, generate disturbances, and can contribute directly to metabolic, physiological, developmental, or behavioral processes. Living organization depends upon continuing ecological interaction.

Ecological Coupling refers here to the organism–organism and organism–environment relations that contribute to the continued organization of a biological system. Such coupling may involve resource exchange, symbiosis, environmental modification, signaling, behavioral interaction, or other recurrent relations through which biological organization is maintained.

Ecological Coupling is analytically distinct from Context in the PSE architecture. Context is the domain-independent relational setting within which organization is distinguished and persists. Ecological Coupling identifies particular biological relations within that Context that contribute to the continuation of living organization. It represents a domain-specific analytical dimension rather than an equivalent of Context itself.

Ecological interaction alone does not establish that interacting entities belong to the same biological individual. Relations may be necessary for persistence while connecting organizations that retain distinct boundaries, developmental histories, or evolutionary continuities.
The relevant issue is which ecological relations contribute *constitutively* to the organization under investigation and at which organizational level their effects occur.

The comparative analysis examines the form, persistence, and organizational significance of these relations across different biological systems. Their relevance to Biological Individuality depends upon how Ecological Coupling relates to Organizational Boundaries, Organizational Integration, Developmental Continuity, Adaptive Persistence, and Evolutionary Continuity.

### 4.7 Evolutionary Continuity

Biological organization also has a transgenerational dimension. Reproduction establishes relations between successive biological organizations, while heredity, variation, and differences in reproductive success contribute to evolutionary continuity and change across generations (Godfrey-Smith, 2009).

Evolutionary Continuity refers to continuity across generations involving reproduction, heredity, variation, differential reproductive success, and evolutionary change. It concerns the relations through which biological characteristics and organizational consequences extend across generations without implying persistence of the same individual organization.

Evolutionary Continuity is analytically distinct from both Organizational Identity and Developmental Continuity.
Organizational Identity concerns continuity through successive states of an organized system. Developmental Continuity concerns continuity across transformations within its biological history. Evolutionary Continuity concerns relations among successive organizations and lineages across generations.

The organizational level at which Evolutionary Continuity is identified requires separate analysis. Reproduction, heredity, variation, and differential success may be organized at levels that do not coincide with those identified through physiological integration, developmental continuity, or ecological coupling. In collective systems especially, evolutionary processes involving constituent organisms do not by themselves establish Evolutionary Continuity of the collective as an evolutionary individual.

The comparative analysis examines where reproduction and heredity occur, how evolutionary continuity is organized across generations, and whether the relevant evolutionary processes coincide with the organizational level at which Biological Individuality is being considered. Evolutionary relevance at a particular level does not by itself establish Biological Individuality at that level.

## 4.8 Analytical Framework

The six dimensions developed in this chapter together constitute the analytical framework for the comparative case studies that follow. Each case is examined in terms of Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity.

Applying the same dimensions across biologically different systems provides a common basis for comparison. The analysis examines how each dimension is realized, at which organizational level it operates, and how the dimensions relate within each case. Particular attention is given to whether they converge upon the same organization or remain distributed across different boundaries and levels.

The resulting profiles are descriptive and comparative. They do not assign scores, establish a hierarchy of biological systems, or presuppose that greater convergence among the six dimensions corresponds to a greater degree of Biological Individuality. Nor does the occurrence of all six dimensions within a case establish that the system constitutes a Biological Individual.

The use of a common framework also imposes an important methodological limitation. Because the same dimensions are deliberately applied to every case, their recurrence across the case studies cannot by itself constitute evidence for a recurring organizational architecture.
Any stronger claim concerning structural recurrence or Organizational Scale Invariance requires independently identifiable correspondences among organizational relations.

Chapters 5 through 8 develop the individual case profiles. Chapter 9 then compares those profiles and asks whether the framework clarifies relations among established concepts of biological individuality, whether recurrent organizational relations can be identified independently of the framework used to describe them, and where the explanatory limits of the proposed analysis become apparent.

# Part III — Comparative Biological Analysis

## Chapter 5 — Case I: The Living Cell

### 5.1 Why the Living Cell?

Every comparative investigation requires a reference case. For the analysis developed here, a free-living unicellular organism provides an appropriate starting point because many processes relevant to biological continuity can be examined in relation to a single cellular organization. Boundary regulation, metabolism, physiological regulation, reproduction, and organism–environment interaction can be analyzed without initially introducing the additional organizational levels characteristic of multicellular organisms or biological collectives (Alberts et al., 2022).

This choice is methodological rather than historical or definitional. It neither identifies the free-living cell as the first biological individual in evolutionary history nor implies that every cell constitutes an equivalent form of individuality. Cells incorporated into multicellular organisms may participate in developmental, physiological, and reproductive organization operating at organismal levels. The reference case is specifically the free-living unicellular organism.

The six dimensions introduced in Chapter 4 can all be investigated in relation to this case, although they do not necessarily describe processes occurring at the same temporal or organizational level. Cellular membranes contribute to Organizational Boundaries; metabolic and regulatory processes contribute to Organizational Integration and Adaptive Persistence; cellular development provides forms of Developmental Continuity; organism–environment relations constitute Ecological Coupling; and reproduction connects cellular organizations across generations within Evolutionary Continuity (Alberts et al., 2022; Godfrey-Smith, 2009).

The free-living unicellular organism provides a reference profile rather than a standard against which other systems are ranked. Chapters 6 through 8 examine how the same analytical dimensions are configured in biofilms, holobionts, and eusocial insect colonies, where relevant processes may be distributed across interacting components, boundaries, and organizational levels.

### 5.2 Cellular Organization

A living cell maintains its organization through continuous material and energetic exchange with its surroundings. Nutrients and other molecular substrates are taken up, metabolic products are released, and cellular constituents are continually synthesized, modified, transported, and degraded. Membrane transport, metabolism, gene expression, molecular turnover, and regulatory processes interact in maintaining cellular organization under these changing conditions (Alberts et al., 2022).

Cellular continuity therefore does not depend upon the permanence of particular material constituents. What persists is an organized set of relations and processes through which cellular

components are continually produced, regulated, replaced, and coordinated while the cell remains functionally connected with its environment.

The free-living cell provides a clear biological case of Persistent Organization as defined in Chapter 3. Its continuity depends upon dynamically maintained boundaries, selective interactions, and coordinated processes while both its material composition and its relations with its Context change through time.

This general organizational profile provides the basis for examining how the six biological dimensions introduced in Chapter 4 are realized in the cellular reference case.

## 5.3 Organizational Boundaries

The plasma membrane provides the principal organizational boundary of the free-living cell. It physically distinguishes intracellular from extracellular conditions while selectively regulating the interactions through which cellular organization is maintained.

Ions, nutrients, signaling molecules, and metabolic products cross this boundary through regulated transport processes. Membrane components are themselves continually synthesized, degraded, and reorganized, while transport proteins, receptors, and, in eukaryotic cells, processes such as endocytosis and exocytosis contribute to the regulation of exchange.
These mechanisms enable cells to maintain chemical gradients, osmotic conditions, metabolic organization, and physiological regulation while remaining materially connected with their surroundings (Alberts et al., 2022).

The cellular membrane therefore exemplifies Organizational Boundaries as defined in Chapter 4: biological boundaries maintain distinguishability through selective regulation rather than through isolation.
In PSE terms, the membrane provides a biological realization relevant to Boundary, while the specific transport and regulatory mechanisms constitute its cellular implementation.

The membrane alone, however, does not establish Biological Individuality. Its significance lies in its participation in a wider organization of metabolic, regulatory, developmental, ecological, and reproductive processes. In the cellular reference case, Organizational Boundaries must be considered in relation to the other dimensions rather than as an independent criterion of individuality.

## 5.4 Organizational Integration

Cellular organization depends upon the coordination of numerous interacting processes. Metabolism, membrane transport, gene expression, molecular synthesis and degradation, energy conversion, and regulatory networks operate through interdependent relations that contribute to the continued organization of the cell. Changes in one process can alter the conditions under which others operate, making cellular persistence dependent upon their continuing coordination (Alberts et al., 2022).

This coordination provides a clear cellular realization of Organizational Integration. The relevant integration does not arise from the mere coexistence of cellular components, but from the regulated relations through which their activities contribute to continued cellular organization.

Organizational Integration at the cellular level must remain analytically distinct from Coherence in the PSE architecture. Coherence refers to the domain-independent compatibility of relations within persistent organization. The metabolic, regulatory, and molecular coordination observed in cells provides a biological realization relevant to that coherence without being identical to the ontological concept itself.

In the free-living unicellular reference case, many of these integrated processes operate within the Organizational Boundaries of a single cell. This makes their organizational relation comparatively clear. It does not imply that Organizational Integration alone establishes Biological Individuality, nor that comparable integration at a collective level necessarily produces a collective biological individual.

The cellular case provides a reference profile for examining how integration is reorganized in the collective cases that follow, where coordinated processes may extend across multiple biological entities while those entities retain substantial organizational independence.

### 5.5 Adaptive Persistence

A free-living cell encounters continual variation in the conditions relevant to its continued organization. Nutrient availability, temperature, osmotic conditions, chemical composition, and other environmental factors can change, while internal disturbances may alter metabolic and physiological states.

Cells respond to such variation through regulatory processes that modify cellular activity while maintaining viable organization. Changes in gene expression, metabolic regulation, membrane transport, stress responses, repair processes, and other physiological adjustments can alter cellular functioning in response to changing conditions (Alberts et al., 2022).

These responses provide a cellular realization of Adaptive Persistence. Continued cellular organization does not require maintenance of an invariant physiological state; it may depend upon regulated change that restores or preserves conditions compatible with cellular viability.

Adaptive Persistence at the cellular level must be distinguished from evolutionary adaptation. The regulatory responses considered here occur during the organizational history of a cell and can contribute to its continued viability without requiring heritable change across generations. Evolutionary consequences of cellular reproduction and variation belong to the separate dimension of Evolutionary Continuity.

The cellular case shows how viable organizational continuity can depend upon regulated change within a persistent biological organization. Adaptive Persistence contributes to the analysis of cellular individuality, but its presence alone does not establish Biological Individuality.

## 5.6 Developmental Continuity

A free-living cell has an organizational history in which successive states remain connected through time. Growth, changes in physiological state, molecular turnover, and preparation for cell division can substantially transform cellular organization while continuity is maintained within the history of the cell.

These temporally connected transformations provide a cellular realization of Developmental Continuity. The relevant continuity lies in the relations through which successive cellular states remain part of an ongoing developmental history, without requiring the cell to remain structurally or physiologically unchanged.

Cell division marks an important transition. Cellular structures, molecular components, and hereditary material contribute to the organization of daughter cells, establishing continuity across cellular generations (Alberts et al., 2022).
This reproductive continuity does not imply that the parent cell and its descendants constitute the same Biological Individual.

Developmental Continuity must therefore be distinguished from both reproductive succession and Evolutionary Continuity. The developmental history of an individual cell concerns transformations within that cellular organization. Cell division generates successor organizations, while Evolutionary Continuity concerns transgenerational relations involving reproduction, heredity, variation, and evolutionary change.

The cellular reference case makes the temporal distinction particularly clear: continuity through developmental change can occur within an individual organization, while reproduction establishes continuity between successive cellular organizations.
These forms of continuity are related, but they should not be conflated when assessing Biological Individuality.

## 5.7 Ecological Coupling

A free-living unicellular organism persists through continuous interaction with its surroundings. Nutrients and other molecular resources must become available to cellular processes, metabolic products are exchanged with the environment, and physical, chemical, and biological conditions influence cellular activity. The organizational continuity of the cell is therefore maintained through relations that extend beyond its Organizational Boundaries (Alberts et al., 2022).

These relations provide a cellular realization of Ecological Coupling. Their significance lies in the contribution of organism–environment interactions to continued cellular organization.
The cell remains distinguishable from its surroundings while depending upon selective exchanges and responses across that distinction.

Ecological Coupling must remain analytically distinct from Context. The environment in which a cell persists contains many conditions and relations, only some of which participate directly in the biological processes relevant to its continued organization.

Ecological Coupling concerns those organism–environment relations whose organizational significance is being investigated within that broader Context.

Dependence upon environmental relations does not by itself diminish cellular individuality, nor does such dependence by itself make environmental components part of the cell.
Organizational membership and ecological dependence therefore remain distinct questions.

The free-living cell provides a comparatively clear case in which extensive ecological coupling coexists with a distinguishable cellular organization.
This profile provides a reference for the collective cases that follow, where ecological relations may become more persistent, distributed, or biologically constitutive and where their relation to Organizational Boundaries and Biological Individuality becomes correspondingly more difficult to determine.

## 5.8 Evolutionary Continuity

Reproduction connects individual cells across generations. Hereditary information and cellular organization contribute to the formation of descendant cells, while variation among descendants provides the basis for differences in reproductive success within cellular populations. The resulting continuity extends beyond the organizational history of any single cell (Godfrey-Smith, 2009).

These transgenerational relations provide a cellular realization of Evolutionary Continuity. The relevant continuity lies in relations among successive cellular organizations and lineages rather than in the uninterrupted persistence of one Biological Individual.

The distinction from Developmental Continuity is therefore essential. Developmental Continuity concerns transformations within the organizational history of a cell. Reproduction generates successor organizations and thereby establishes relations across cellular generations.
Evolutionary Continuity concerns how reproduction, heredity, variation, and differential reproductive success are organized across those generations.

In the free-living unicellular reference case, the organizational level at which reproduction occurs corresponds closely to the level at which the cell is otherwise analyzed as a persistent biological organization. This correspondence makes the relation between cellular organization and evolutionary processes comparatively clear, but it does not eliminate the distinction between individual and lineage continuity.

The cellular case provides a reference for the collective systems examined in subsequent chapters. In those cases, reproduction and evolutionary change among constituent organisms need not imply reproduction or Evolutionary Continuity of the collective organization itself.

## 5.9 Organizational Profile

The preceding analyses establish a descriptive organizational profile for the free-living unicellular reference case across the six analytical dimensions introduced in Chapter 4.

| Organizational Dimension | Free-Living Unicellular Reference Case |
|---|---|
| Organizational Boundaries | Membrane-based and selectively regulated boundary through which cellular organization remains distinguishable while interacting with its environment |
| Organizational Integration | Coordinated and interdependent metabolic, regulatory, molecular, and transport processes contributing to continued cellular organization |
| Adaptive Persistence | Regulatory responses maintain or restore viable organizational continuity under changing internal and external conditions |
| Developmental Continuity | Temporal continuity across growth and changing cellular states within the organizational history of the cell; distinct from reproductive succession through cell division |
| Ecological Coupling | Direct and continuous organism–environment relations contributing to continued cellular organization |
| Evolutionary Continuity | Transgenerational continuity through reproduction, heredity, variation, and evolutionary processes across cellular lineages |

This profile serves as a descriptive reference for the case studies that follow. The same dimensions are applied to biofilms, holobionts, and eusocial insect colonies in order to examine how their organizational relations are configured and at which organizational levels they operate.
The cellular profile functions as a common point of comparison, not as a standard or scale of Biological Individuality.

## 5.10 Evaluation

The free-living unicellular organism provides a comparatively clear reference case for examining the six organizational dimensions developed in Chapter 4. Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, and Ecological Coupling can be analyzed in relation to the continuing organization of the cell, while Evolutionary Continuity connects successive cellular organizations across generations.

The resulting profile does not imply that these dimensions constitute a set of necessary or sufficient criteria for Biological Individuality. Nor does their relatively clear relation in the unicellular case establish that they must converge at the same organizational level in other biological systems.
The significance of the cellular case is methodological: it provides a reference configuration against which differently organized biological systems can be compared.

The following case studies apply the same analytical dimensions to biofilms, holobionts, and eusocial insect colonies. In these systems, organizational processes may be distributed among multiple interacting components, may operate across different organizational levels, and may identify boundaries or continuities that do not coincide.

The comparison asks how the organizational dimensions relevant to Biological Individuality are configured beyond the unicellular reference case and how those configurations bear upon the attribution of individuality.
This question remains open for the comparative analysis that follows.

# Chapter 6 — Case II: Biofilms

## 6.1 Why Biofilms?

Biofilms are communities of microorganisms associated with surfaces or interfaces and embedded, wholly or partly, within an extracellular matrix produced by their constituent cells. Within this environment, spatial differentiation, metabolic interactions, chemical signaling, and collective responses can contribute to a persistent organization that extends beyond the activities of individual cells.
Such organization occurs across diverse natural, host-associated, clinical, and engineered environments, where biofilms participate in processes ranging from biogeochemical cycling and host–microbe interactions to persistent infections and industrial systems (Flemming et al., 2016).

This combination of cellular and collective organization makes biofilms particularly informative for the problem of biological individuality. Constituent cells retain their own cellular organization and reproductive capacities, while their interactions with other cells and the extracellular matrix can generate collective structures and coordinated activities that persist over time.
Biofilms provide a useful first comparison with the free-living unicellular reference case developed in Chapter 5: organization now extends across interacting cells while cellular organization remains identifiable within the collective.

The six dimensions introduced in Chapter 4 can be used to examine how organization is distributed across these cellular and collective levels. The central question is how such collective organization bears upon the attribution of biological individuality to the biofilm itself.

## 6.2 Biofilm Organization

Biofilm development commonly involves microbial attachment to a surface or interface, production of extracellular matrix components, cellular proliferation, and progressive modification of the local environment. As the biofilm develops, the matrix provides a structured extracellular environment through which cells interact with one another and with surrounding conditions. Gradients of oxygen, nutrients, metabolites, and signaling molecules can generate spatial heterogeneity, while metabolic interactions and differentiated physiological states contribute to organization across the microbial community (Flemming et al., 2016).

This organization remains dynamic throughout the life of the biofilm. Cells divide, change physiological state, move within or detach from the biofilm, and die, while matrix components are continually produced and modified. The composition and spatial structure of the community may therefore change considerably while aspects of collective organization persist.
As in the cellular reference case, material or component turnover need not coincide with loss of organization; in a biofilm, however, persistence may involve relationships distributed among many cells and their extracellular matrix.

Biofilms extend the analysis of Persistent Organization beyond the single-cell reference case. The relevant question is whether persistence at the collective level supports the attribution of a

distinct biological identity, or whether it remains primarily an outcome of interacting cellular individuals.
That question cannot be answered from persistence alone and will be examined through the six organizational dimensions in the sections that follow.

## 6.3 Organizational Boundaries

The boundary organization of a biofilm differs fundamentally from the membrane-based boundary of the unicellular reference case. A biofilm does not generally possess a single enclosing structure equivalent to a cellular membrane. Its interface with the surrounding environment arises from the spatial organization of cells, extracellular matrix, chemical gradients, and local physical conditions. The extracellular matrix contributes to this organization by retaining water, affecting diffusion and chemical gradients, providing mechanical cohesion, and modifying exposure to environmental stresses (Flemming et al., 2016).

The resulting interface may remain spatially irregular and dynamically reorganized. Cells can join or leave the biofilm, portions may detach, and growth or environmental change can alter its shape and internal structure. A biofilm boundary can therefore be organizationally consequential without defining membership as sharply as the membrane of a free-living unicellular organism.

This difference is important for the analysis of biological individuality. An Organizational Boundary at the collective level need not take the form of a single physical enclosure, but neither does every persistent interface establish a distinct biological individual.
In the biofilm case, the relevant question is how far the spatial and matrix-mediated organization of interactions distinguishes the collective as a persistent system from its surrounding Context.

## 6.4 Organizational Integration

Organizational Integration in biofilms arises through interactions among cells and between cells and the extracellular matrix. Chemical signaling, spatial differentiation, metabolic exchange, and matrix production can coordinate processes across parts of the community.
Quorum sensing provides one mechanism through which local cellular activity may acquire collective effects: signaling molecules produced by cells can influence gene expression in other cells as their local concentration changes, thereby affecting processes such as matrix production, motility, virulence, or dispersal. The occurrence and function of such signaling vary substantially among microbial species and biofilm systems (Waters & Bassler, 2005; Flemming et al., 2016).

Integration can also arise through metabolic relations. Gradients of oxygen, nutrients, and metabolic products create heterogeneous micro-environments within biofilms, allowing different cells or regions to perform complementary metabolic activities. Products generated by one population may serve as substrates for another, establishing functional dependencies that extend beyond individual cells.
Such interactions can contribute to collective persistence without eliminating the cellular organization of the participating microorganisms (Flemming et al., 2016).

The resulting configuration differs from the unicellular reference case. Cellular processes there are integrated within one cellular system; in a biofilm, some organizational relations extend among multiple cells while those cells retain their own boundaries, metabolic organization, and capacity for reproduction. Organizational Integration can therefore occur simultaneously at more than one level.
Whether integration at the collective level is sufficient to support a corresponding level of biological individuality remains a separate question.

### 6.5 Adaptive Persistence

Biofilm organization can contribute substantially to microbial persistence under changing or adverse environmental conditions. The extracellular matrix can modify diffusion and exposure to antimicrobial compounds, while spatial and physiological heterogeneity creates local micro-environments in which cells differ in metabolic activity, growth rate, and susceptibility to stress. Physiological responses, altered gene expression, and the presence of slow-growing or dormant subpopulations may further increase the capacity of cells within a biofilm to survive disturbances that would affect planktonic populations differently (Flemming et al., 2016).

Such persistence can also involve reorganization. Environmental change may alter metabolic activity, matrix production, spatial structure, or the relative abundance of microbial populations, while dispersal and subsequent growth can establish biofilm organization elsewhere.
The continued or renewed presence of a biofilm therefore need not depend upon maintaining an unchanged collective state.

These properties make biofilms informative for Adaptive Persistence, but they require careful interpretation. Increased tolerance at the biofilm level can result from several interacting cellular, physicochemical, and collective mechanisms and does not by itself establish adaptation by the biofilm as a biological individual.
The relevant question is whether responses to changing Context contribute to the maintenance or restoration of a distinguishable collective organization, and at which organizational level that adaptive persistence should be attributed.

### 6.6 Developmental Continuity

Biofilms change over time through processes that may include cellular attachment, proliferation, matrix production, spatial restructuring, detachment, and dispersal. These processes can produce recognizable temporal patterns of biofilm development, although their sequence and relative importance vary among organisms and environmental conditions.
Biofilm development should therefore not be understood as a single universal life cycle through which every biofilm passes (Flemming et al., 2016).

Within an established biofilm, temporal change occurs at several interacting levels. Constituent cells divide, die, alter their physiological states, or leave the community, while matrix production, spatial structure, metabolic relations, and species composition may also change. Some

collective relationships can persist through these transformations, allowing aspects of biofilm organization to continue despite substantial turnover among cells and local structures.

Developmental Continuity at the collective level depends upon the temporal connection between successive states of biofilm organization. This must be distinguished from the developmental histories of constituent cells and from the formation of a new biofilm following dispersal. Dispersal and recolonization may transmit cells and organizational capacities to another location, but they do not by themselves establish that the resulting biofilm is the continuation of the same biological individual.
The biofilm case raises the question of how organizational continuity across changing collective states bears upon the attribution of a distinct developmental history to the collective itself.

## 6.7 Ecological Coupling

Biofilm organization is closely connected to the environmental conditions under which it develops and persists. Availability and transport of nutrients and oxygen, hydrodynamic conditions, surface properties, temperature, and interactions with other organisms can influence biofilm composition, spatial structure, and physiological activity. At the same time, biofilm activity can alter local chemical gradients, nutrient flows, physical surfaces, and other features of the surrounding environment (Flemming et al., 2016).

This interaction can generate continuing feedback between biofilm organization and local environmental conditions. Changes in the environment affect the organization of the biofilm, while metabolic activity, matrix production, resource consumption, and other microbial processes modify conditions subsequently encountered by the community.
Ecological Coupling therefore concerns more than exposure to an external environment: it describes organized relations through which biofilm persistence and environmental conditions can become dynamically interdependent.

The analytical significance of this coupling depends upon its contribution to the persistence of a distinguishable collective organization. Strong environmental dependence does not in itself establish biological individuality, just as modification of the environment does not make that environment part of the biofilm.
The relevant issue is whether particular organism–environment relations participate in maintaining the biofilm as a persistent organizational configuration while the distinction between that organization and its Context remains identifiable.

## 6.8 Evolutionary Continuity

The evolutionary status of biofilms requires a distinction between evolutionary processes occurring within a biofilm and evolution of the biofilm as a collective unit. Constituent microorganisms participate in reproductive lineages through heredity, variation, and differential reproductive success. Their organization within a biofilm can alter the conditions under which these processes occur by changing spatial relationships, resource availability, competition, cooperation, and exposure to environmental pressures.

Selection can operate on traits expressed in the biofilm environment without implying that the biofilm itself constitutes an evolutionary individual. Matrix production, metabolic interactions, signaling, and other collective characteristics may affect the reproductive success of constituent lineages, while mutation, migration, competition, and differences in genetic relatedness can generate divergent evolutionary interests within the same biofilm. Attributing evolutionary individuality at the collective level would require additional evidence that reproduction, heredity, variation, and differential reproductive success are organized at that level (Godfrey-Smith, 2009).

Evolutionary Continuity in biofilms is clearest at the level of the reproducing microbial lineages. Biofilm organization can shape the ecological and selective conditions under which those lineages persist and evolve, but such effects do not by themselves establish a biofilm-level lineage.
This distinguishes Evolutionary Continuity from the collective persistence, integration, and developmental change examined in the preceding sections.

The biofilm case shows why the six analytical dimensions should remain distinct. Collective organization may be substantial in several dimensions while the attribution of evolutionary individuality remains conditional upon the particular biological system and the evolutionary processes involved.

## 6.9 Organizational Profile

The preceding analysis yields the following descriptive profile of biofilm organization:

| **Organizational Dimension** | **Biofilm** |
|---|---|
| Organizational Boundaries | Spatially and matrix-mediated interface; dynamic and variably defined |
| Organizational Integration | Functional relations distributed among interacting cells and extracellular matrix |
| Adaptive Persistence | Collective persistence supported by interacting cellular, physicochemical, and organizational responses |
| Developmental Continuity | Temporal continuity among changing collective states; distinct from cellular succession and recolonization following dispersal |
| Ecological Coupling | Dynamic interdependence between biofilm organization and local environmental conditions |
| Evolutionary Continuity | Clearest in constituent microbial lineages; collective organization can modify selective conditions without necessarily constituting a biofilm-level lineage |

Compared with the free-living unicellular reference case, biofilm organization is distributed across multiple cells and their extracellular matrix while cellular organization remains identifiable within the collective. The six dimensions can be applied at the collective level, but they do not converge there with equal clarity. Boundary formation, integration, persistence, developmental change, ecological coupling, and evolutionary continuity each raise different questions about the organizational level to which they should be attributed.

The profile does not establish the biofilm as a biological individual. It identifies a configuration in which persistent collective organization coexists with the continued organization of constituent cells, leaving the attribution of collective biological individuality dependent upon the particular biofilm and the organizational relations under consideration.

### 6.10 Evaluation

Biofilms provide the first comparative case in which persistent biological organization is examined across multiple interacting cells while the constituent cells remain identifiable as organized biological systems in their own right.
The analysis shows that the six dimensions do not converge uniformly at the collective level: boundary organization remains comparatively diffuse; integration and adaptive persistence arise through interacting cellular, physicochemical, and collective processes; developmental continuity can be identified across changing collective states without necessarily extending through dispersal; ecological coupling operates strongly at the collective level; and evolutionary continuity remains most clearly attributable to reproducing microbial lineages.

This configuration complicates the attribution of biological individuality. A biofilm cannot adequately be characterized by considering its constituent cells in isolation, because interactions among cells, extracellular matrix, and local environmental conditions contribute to persistent collective organization. Yet the existence of such organization does not by itself establish the biofilm as a distinct biological individual. The configuration of these organizational relations can also vary among different biofilm systems.

The biofilm case supports a distinction between collective organization and collective individuality. Persistent organization can arise through relations distributed across multiple biological entities without requiring those entities to lose their own organizational identities. Whether Biological Individuality can also be attributed to the resulting collective remains a separate question requiring comparative assessment of how these organizational dimensions are configured and related at the collective level.

This distinction provides the point of departure for the analysis of holobionts in Chapter 7. Host–microbial associations introduce a different configuration of biological relations, allowing the same analytical dimensions to be examined where the persistence and functioning of a host may depend upon interactions with biologically distinct partners.

## Chapter 7 — Case III: Holobionts

### 7.1 Why Holobionts?

Multicellular organisms live in persistent association with diverse microbial communities whose activities can influence host nutrition, metabolism, development, immune function, and interactions with the environment. The term *holobiont* has come to designate a host together with its associated microorganisms, drawing attention to biological relationships that can contribute substantially to host functioning while differing greatly in duration, specificity, dependence, and mode of transmission (Bordenstein & Theis, 2015; Lloyd-Price et al., 2016).

These associations pose a distinctive problem for biological individuality. A host possesses its own developmental and evolutionary continuity, yet some aspects of its organization may depend upon interactions with microorganisms that have their own boundaries, reproductive histories, and ecological relationships. Microbial partners may be stably associated with the host,

acquired repeatedly from the environment, transmitted between generations, or replaced over the host's lifetime. The organizational significance of the microbiota therefore cannot be inferred from association alone.

The central question is how relations between a host and its associated microorganisms contribute to collective organization and how that organization bears upon the attribution of Biological Individuality to the combined system.
Different concepts of individuality can yield different answers because physiological integration, developmental continuity, ecological coupling, and evolutionary continuity need not coincide at the same organizational level.

Holobionts provide a particularly demanding comparison with the unicellular and biofilm cases. In the unicellular reference case, the six dimensions converge comparatively clearly within one cellular system. Biofilms showed that collective organization can coexist with persistent cellular organization while the dimensions diverge in their attribution across organizational levels. Host–microbial associations add a further possibility: processes contributing to the persistence and functioning of one biological system may depend upon interactions with other biological entities whose organizational and evolutionary histories remain partly distinct.

The following analysis applies the same six dimensions without assuming in advance that the host and its microbiota constitute either a single biological individual or merely an ecological assemblage. The question is how these dimensions are configured in host–microbial associations and what that configuration permits us to conclude about the location and extent of biological individuality.

### 7.2 Host-Microbiome Organization

Host-associated microbial communities participate in numerous processes that can affect host physiology. Depending on the biological system, microbial activities may contribute to nutrient acquisition and metabolism, development, immune function, protection against pathogens, and other aspects of host functioning. The host in turn provides microbial populations with spatially structured habitats, nutrients, chemical conditions, and physiological environments that influence their establishment and persistence (McFall-Ngai et al., 2013; Bordenstein & Theis, 2015).

These relations can produce recurring patterns of host–microbial organization, but their organizational significance varies considerably. Some microbial associations are transient, whereas others persist through substantial portions of the host's lifetime. Some involve highly specific partners; others permit extensive taxonomic replacement while particular functions remain comparatively stable. Microorganisms may be acquired horizontally from the environment, transmitted between hosts, or passed between generations through different forms of vertical or mixed transmission (Bordenstein & Theis, 2015; Douglas & Werren, 2016).
A host-associated microbiota is not necessarily a fixed set of organisms accompanying the host through its developmental history.

This variability is central to the problem of biological individuality. Microbial contributions may be important, or even necessary, for particular host functions without implying that host and

microorganisms constitute a single organizational identity. Conversely, persistent dependence, reciprocal regulation, or reliable transmission may create organizational relations whose significance cannot be captured by treating host and microbial partners entirely independently. The analytical task is to determine how such relations are organized and at which level their persistence should be attributed.

The holobiont case requires a distinction between functional contribution, organizational dependence, and collective organization. These relations may overlap, but they should not be treated as equivalent.
The six dimensions developed in Chapter 4 provide a way to examine where host and microbial organization become interconnected and where their respective organizational histories remain distinct.

## 7.3 Dynamic Membership

Host-associated microbial communities can change substantially during the lifetime of a host. Individual microorganisms may be lost and replaced, relative abundances can shift, and taxonomic composition may vary with development, diet, environment, physiological state, and other conditions. At the same time, some microbial functions and patterns of interaction can remain comparatively stable despite changes in the organisms through which they are realized (Human Microbiome Project Consortium, 2012; Lloyd-Price et al., 2016).

This combination of compositional change and functional continuity raises a question already encountered in the cellular and biofilm cases: *what must persist for organizational continuity to be maintained?* In host–microbial associations, persistence cannot automatically be identified with continued membership of the same microbial organisms or taxa.
It may instead involve the maintenance or restoration of particular functions, interactions, or relational configurations despite turnover among participating microorganisms.

Functional continuity, however, is not sufficient by itself to establish continuity of a holobiont as a biological individual. Similar functions may be performed by different microorganisms, and microbial replacement may occur without implying that the incoming organisms inherit membership in a single continuing collective identity. The relevant issue is whether changes in microbial composition preserve an organization of host–microbial relations that contributes to the continued organization of the biological system under consideration.

Dynamic membership makes the level of persistence itself an empirical question. Host continuity may be maintained despite microbial turnover; particular host–microbial relationships may persist or recur; and some microbial lineages may follow trajectories largely independent of the host.
These forms of continuity should remain analytically distinct unless independent evidence supports their attribution to a persistent collective organization.

## 7.4 Boundary Problems

Host–microbial associations make the location of biological boundaries particularly difficult to determine. The anatomical boundary of a host remains biologically important, yet many microorganisms associated with the skin, respiratory tract, digestive tract, and other host interfaces participate in processes that can affect metabolism, immune function, development, and protection against pathogens (Gilbert et al., 2012; McFall-Ngai et al., 2013). Their location relative to the host's anatomical surfaces therefore does not by itself determine their organizational relation to the host.

Neither proximity nor functional contribution is sufficient to establish organizational membership. Host-associated microorganisms differ substantially in persistence, specificity, dependence, transmission, and degree of physiological integration. Some associations are transient or readily replaceable, whereas others participate recurrently or persistently in processes important to host organization.
The boundary relevant to biological individuality cannot be established simply by cataloguing the microorganisms present at a particular moment.

Different concepts of individuality emphasize different aspects of this problem. Physiological and immunological approaches focus on functional integration and processes of biological inclusion and exclusion; ecological approaches emphasize persistent interaction networks; evolutionary approaches ask how reproduction, heredity, and selection are organized across host and microbial partners participate in sufficiently aligned processes of reproduction, heredity, and selection (Pradeu, 2012; Skillings, 2016; Godfrey-Smith, 2009; Queller & Strassmann, 2009). These perspectives need not identify the same boundary because they address different forms of biological organization.

An Organizational Boundary, as used in this analysis, cannot be reduced to anatomical enclosure. It concerns the maintained distinction through which interactions contributing to the persistence of a biological organization are selectively structured in relation to its Context. Anatomical structures can participate importantly in maintaining such a distinction, while organizationally consequential relations may also involve biological entities located across or beyond those structures.

This does not imply that every organism contributing to host persistence becomes part of the same biological individual. Environmental resources, prey, mutualists, competitors, and other organisms may be indispensable or highly consequential while remaining organizationally distinct.
The boundary problem is more specific:

> *which host–microbial relations participate in maintaining a distinguishable organization, and do those relations justify extending biological individuality beyond the host itself?*

## 7.5 Units of Selection

Evolutionary individuality raises a more specific question than physiological or ecological integration: whether a biological entity participates as a distinct unit in Darwinian processes

involving reproduction, heredity, variation, and differential reproductive success. Applied to holobionts, the question is not simply whether host and microorganisms affect one another's fitness, but whether their association generates heritable variation upon which selection can act at the collective level (Godfrey-Smith, 2009).

Host–microbial associations present difficulties for such an interpretation because the participating lineages need not share the same mode of transmission. Host genomes are transmitted through host reproduction, whereas many associated microorganisms are acquired horizontally from the environment or from other hosts and may change substantially between generations. In such cases, physiological or functional integration within a host lifetime does not automatically generate corresponding evolutionary continuity at the host–microbiome level (Douglas & Werren, 2016).

The evolutionary status of holobionts nevertheless remains dependent upon the particular biological association. Hologenome approaches have emphasized cases in which recurrent host–microbial associations, reliable transmission, or consistent reconstruction of functionally significant microbial communities may allow selection to involve properties of the combined system (Rosenberg & Zilber-Rosenberg, 2014; Bordenstein & Theis, 2015).
Critics emphasize that variation in microbial composition, horizontal acquisition, and potentially divergent evolutionary interests can prevent such associations from functioning as a distinct Darwinian unit (Douglas & Werren, 2016). Functional cooperation or reciprocal dependence alone is insufficient to establish a holobiont as a unit of selection.

Evolutionary Continuity must be assessed separately from the other organizational dimensions. A host–microbial association may exhibit substantial physiological integration, developmental dependence, or ecological coupling while evolutionary continuity remains concentrated in the distinct reproductive lineages of host and microorganisms. In other cases, more reliable transmission and alignment of evolutionary interests may strengthen the case for collective evolutionary individuality.
The relevant attribution is empirical and association-specific, rather than a property that follows from the category holobiont itself.

## 7.6 Biological Individuality?

The preceding analysis does not support a single answer to the question of whether holobionts constitute biological individuals. Host–microbial associations differ substantially in the persistence, specificity, transmission, and functional significance of their constituent relationships. The attribution of individuality must depend upon the organizational configuration of a particular association rather than upon its classification as a holobiont.

Across the six dimensions, this configuration can be uneven. Organizational boundaries may remain centered primarily on the host while functionally significant relations extend to associated microorganisms. Organizational integration can become substantial where microbial activities contribute recurrently to host physiology, yet microbial membership may remain dynamic. Adaptive Persistence and Developmental Continuity may involve host–microbial interactions without requiring continuity of the same microbial partners. Ecological Coupling can operate strongly across the combined association, while Evolutionary Continuity may remain

concentrated in distinct host and microbial lineages unless transmission and evolutionary interests become sufficiently aligned.

These differences make it possible for host and microbial partners to participate in persistent collective organization without all dimensions converging upon a single collective individual. Functional contribution, reciprocal dependence, and Organizational Integration may each be relevant to collective organization, but none independently establishes Biological Individuality. Their significance must be assessed through their relations to the other organizational dimensions and the organizational levels at which those dimensions are realized.

Holobionts expose a central feature of biological individuality: its organizational dimensions can overlap without being coextensive. The question is not whether every holobiont is an individual, but how the organizational dimensions of a particular host–microbial association are configured and whether Biological Individuality can be warranted at the collective level.

## 7.7 Organizational Profile

The preceding analysis yields the following descriptive profile of host–microbial organization:

| **Organizational Dimension** | **Holobiont** |
|---|---|
| Organizational Boundaries | Primarily host-centered anatomical regulation, with organizationally consequential relations extending to associated microorganisms |
| Organizational Integration | Variable host–microbial functional integration; microbial membership may remain dynamic |
| Adaptive Persistence | Host persistence can depend upon microbial contributions without requiring persistence of the same microbial partners |
| Developmental Continuity | Host developmental continuity may incorporate recurrent microbial contributions despite turnover or reacquisition |
| Ecological Coupling | Strong interaction among host, microbial partners, and surrounding environmental conditions |
| Evolutionary Continuity | Often distributed among distinct host and microbial lineages; collective continuity depends upon transmission and alignment of evolutionary processes |

Unlike the free-living unicellular reference case, the six dimensions do not necessarily identify the same organizational unit. Some remain centered primarily on the host, others extend across host–microbial relations, and evolutionary continuity may remain distributed among distinct reproductive lineages. Their configuration can also differ substantially among host–microbial associations.

The profile does not classify the holobiont as a biological individual. It identifies the organizational relations that must be evaluated in determining whether a particular host–microbial association warrants attribution of individuality at the collective level.

## 7.8 Evaluation

The holobiont case extends the result obtained from biofilms. The six organizational dimensions need not identify the same biological unit, and their divergence cannot be represented adequately as a simple difference in the degree of integration. In host–microbial associations, boundaries may remain centered primarily on the host while physiologically important relations extend to microbial partners; developmental and adaptive processes may depend upon those

relations despite changing microbial membership; ecological coupling may encompass the combined association; and evolutionary continuity may remain divided among distinct reproductive lineages.

This configuration shows why dependence and integration must be distinguished from organizational membership and biological individuality. A microbial partner may contribute substantially, or even indispensably, to host persistence without thereby becoming part of the same biological individual.
Conversely, persistent relations among organizationally distinct partners may form collective organizational configurations for which a purely host-centered account is incomplete. The organizational status of the association depends upon the particular relations through which its components are maintained, coordinated, and reproduced over time.

The comparative progression from the unicellular reference case through biofilms to holobionts reveals increasing differentiation in the attribution of the six dimensions, without implying a linear increase in organizational complexity or individuality. Biological individuality becomes problematic where boundaries, integration, persistence, developmental continuity, ecological coupling, and evolutionary continuity do not converge upon the same biological entity.
The next case examines a different configuration: eusocial insect colonies, in which collective organization can involve persistent division of labour, coordinated reproduction, and colony-level continuity among highly differentiated constituent organisms.

## Chapter 8. Eusocial Insect Colonies

### 8.1 Why Eusocial Colonies?

Eusocial insect colonies provide a particularly informative case for the study of biological individuality because organization extends across numerous multicellular organisms while those organisms retain their own physiological and developmental organization. In ants, termites, many bees, and certain wasps, division of labour, communication, brood care, resource acquisition, nest maintenance, and reproduction can generate persistent colony-level organization extending beyond the activities of any individual member (Hölldobler & Wilson, 2009; Seeley, 2010).

This organization has long motivated comparisons between eusocial colonies and multicellular organisms. The concept of the superorganism emphasizes the extent to which reproductive specialization and coordinated activity can make a colony function as an integrated biological system (Wheeler, 1911; Hölldobler & Wilson, 2009). Evolutionary analyses have subsequently examined more precisely the conditions under which such integration can support colony-level individuality, including reproductive division of labour, cooperation and conflict, relatedness, and the organization of selection across levels (Bourke, 2011; Queller & Strassmann, 2009).

Eusocial colonies nevertheless retain a feature that makes the attribution of individuality analytically difficult. Their constituent insects remain multicellular organisms with their own anatomical boundaries, physiological processes, developmental histories, and behavioral capacities. Colony-level organization develops through persistent relations among organisms that remain biologically organized entities in their own right. The existence of extensive

collective coordination cannot by itself determine whether biological individuality should also be attributed to the colony.

This makes eusocial colonies importantly different from the preceding cases. Biofilms showed that collective organization can arise among cells without the six organizational dimensions necessarily converging at the collective level. Holobionts showed that functionally important and even indispensable relations among different biological partners do not by themselves determine organizational membership or collective individuality. Eusocial colonies introduce another configuration: extensive division of labour and reproductive specialization can organize the activities of multiple organismal individuals into a persistent collective system.

The question is how the six organizational dimensions identified in Chapter 4 are distributed between colony members and colony-level organization. Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity may be attributable to colony-level organization to different degrees and through different biological mechanisms.
Their configuration must be examined before colony-level biological individuality can be assessed.

Eusocial colonies provide a fourth comparative case in which the relation between Persistent Organization and Biological Individuality can be investigated without assuming in advance that collective organization either constitutes or excludes collective individuality.

## 8.2 Organizational Integration

Eusocial insect colonies can exhibit extensive coordination among individuals through division of labour, communication, and reciprocal behavioral responses. Colony members may participate in brood care, foraging, nest construction and maintenance, defense, resource processing, and environmental regulation. These activities can become functionally interdependent because successful performance of one task affects the conditions under which other colony processes are maintained (Hölldobler & Wilson, 2009).

Division of labour is an important component of this integration. In many eusocial insects, individuals differ in the tasks they perform according to age, morphology, physiological state, experience, or changing colony conditions. Task allocation can also remain flexible, allowing workers to shift their activities when colony requirements change. The organization of labour is produced through interactions between individual characteristics and colony conditions rather than through a fixed allocation of functions to every colony member (Robinson, 1992).

Communication and local interaction contribute to the coordination of these activities. Chemical signals, tactile interactions, vibrational cues, and behavioral feedback can alter the probability that individuals perform particular tasks or respond to changing local conditions. In well-studied systems such as honeybee colonies, distributed interactions can generate collective decisions concerning resource exploitation, nest-site selection, and other colony activities without requiring centralized control (Seeley, 2010).

Organizational Integration at the colony level arises through relations among organisms that remain physiologically and behaviorally organized in their own right. This differs from the free-living unicellular reference case, where the relevant processes are coordinated within one cellular system, and from biofilms, where collective integration occurs primarily among microbial cells and their extracellular environment. In eusocial colonies, integration involves the coordination of multicellular organisms whose activities can become differentiated and mutually dependent within the collective.

The persistence of colony organization can also exceed the participation of particular workers. Individual colony members die, new individuals emerge, and task distributions change while patterns of division of labour, communication, brood care, and resource regulation may continue. Such continuity indicates that colony-level integration can persist despite turnover among participating organisms. It does not imply that individual insects are equivalent to replaceable cellular components, because their physiological organization, developmental trajectories, and behavioral capacities remain distinct.

Organizational Integration is clearly present at the colony level, although its character and extent vary among eusocial species and colony states. Its significance for biological individuality depends upon how this integration relates to the other organizational dimensions.
Extensive coordination establishes the biological importance of colony-level organization, while the attribution of colony-level individuality requires the broader comparative analysis developed in the following sections.

### 8.3 Developmental Continuity

Eusocial colonies have developmental histories that extend beyond the development of their individual members. Colonies are established, grow, change in demographic composition and division of labour, produce reproductive individuals, and may eventually decline or cease to exist. Throughout these changes, colony organization can persist despite the birth, development, and death of many of the organisms through which it is realized (Hölldobler & Wilson, 2009; Bourke, 2011).

This temporal organization differs from the developmental continuity of a multicellular organism. Individual insects undergo their own organismal development, while colony-level organization is maintained through interactions among successive and overlapping generations of such individuals. Developmental processes occur simultaneously at more than one organizational level: individual organisms develop within a social environment whose organization can itself change and persist through time.

Caste differentiation illustrates the interaction between these levels. In many eusocial species, developmental pathways leading to reproductive and non-reproductive phenotypes are influenced by combinations of genetic, nutritional, physiological, environmental, and social factors. The relative importance of these influences differs substantially among taxa and should not be represented as a single developmental mechanism characteristic of eusociality as a whole (Wilson, 1971; Hölldobler & Wilson, 2009; Bourke, 2011).

Colony organization can in turn influence the conditions under which new individuals develop. Brood care, food provisioning, nest conditions, social interactions, and chemical signals may affect developmental trajectories, while newly developed individuals subsequently enter existing patterns of communication and division of labour.
Colony continuity can involve the recurrent incorporation of newly developed organisms into an organization that existed before their participation.

This continuity must be distinguished from colony reproduction. The production of reproductive individuals, swarming, budding, colony fission, or other modes of colony founding can establish new colonies, depending upon the species. Such processes may transmit biological and organizational characteristics across colony generations, but they do not imply that a newly founded colony is the same biological individual as its colony of origin.
Developmental Continuity within a colony and reproductive continuity between colonies represent distinct temporal relations.

Developmental Continuity at the colony level can be identified where successive colony states remain connected through the maintenance and reorganization of social relations despite turnover among individual members. This continuity is compatible with the continued developmental individuality of the constituent insects.
Whether it contributes to colony-level biological individuality depends upon its relation to Organizational Boundaries, Organizational Integration, Adaptive Persistence, Ecological Coupling, and Evolutionary Continuity.

## 8.4 Organizational Boundaries

Eusocial colonies present a distinctive configuration of biological boundaries because colony organization extends across numerous physically separate organisms. Each insect retains its own anatomical boundary, while interactions among colony members generate an additional level of organization whose extent cannot be identified simply with the bodies of its constituent organisms.

The nest can contribute substantially to this organization. It provides spatial structure for brood care, food storage, communication, defense, and, in many species, regulation of local environmental conditions. Colony activity nevertheless commonly extends beyond the nest through foraging, resource acquisition, territorial interactions, mating, and other relations with the surrounding environment. The physical limits of the nest do not necessarily coincide with the organizational limits of the colony (Hölldobler & Wilson, 2009).

Recognition and communication processes can contribute more directly to the regulation of colony membership and interaction. In many social insects, chemical cues are involved in discrimination between nestmates and non-nestmates, thereby affecting aggression, cooperation, resource exchange, and access to colony resources. Cuticular hydrocarbons provide an important mechanism of such recognition in many species, although recognition systems and their reliability vary among taxa and ecological conditions (van Zweden & d'Ettorre, 2010).

These processes illustrate why Organizational Boundaries at the colony level cannot be reduced to spatial enclosure. Colony members may repeatedly cross the physical limits of a nest while remaining participants in colony organization, whereas organisms located nearby or even within the same physical environment need not thereby become colony members.
The relevant boundary is expressed partly through regulated relations that distinguish participation in colony organization from interactions belonging to its wider ecological Context.

This distinction does not make every relation contributing to colony persistence part of the colony itself. Food sources, nesting materials, mutualists, competitors, predators, and features of the physical environment may strongly affect colony persistence while remaining outside its organizational membership.
As in the holobiont case, causal importance and ecological dependence must be distinguished from organizational membership.

Organizational Boundaries in eusocial colonies are distributed across anatomical, spatial, behavioral, and recognition-mediated processes. Their collective organization can remain distinguishable despite movement of colony members and continuing exchange with the environment, but the resulting boundary is different in character from the membrane-based boundary of the unicellular reference case.
Whether such boundary regulation contributes to colony-level biological individuality must be assessed together with the other organizational dimensions.

### 8.5 Evolutionary Continuity

Eusocial colonies are especially important for the analysis of Evolutionary Continuity because reproduction can become strongly differentiated among colony members. In many eusocial systems, reproductive activity is concentrated in one or a limited number of reproductive individuals, while workers contribute primarily through brood care, foraging, defense, nest maintenance, and other activities affecting the reproductive success of the colony. The extent and organization of this reproductive division of labour vary substantially among eusocial taxa (Hölldobler & Wilson, 2009; Bourke, 2011).

Kin-selection theory explains how apparently costly helping behaviour can evolve when its effects on genetically related recipients contribute to inclusive fitness (Hamilton, 1964a, 1964b). High relatedness can therefore facilitate the evolution of cooperation and reproductive specialization, although relatedness alone does not determine the degree of colony integration or establish the colony as an evolutionary individual. Conflict over reproduction and resource allocation can persist within highly cooperative societies, and its extent differs among species and social systems (Bourke, 2011).

Evolutionary analyses formulated in terms of multilevel selection address the same general problem from a different analytical perspective by examining how selection can operate on variation within and among groups. Where colony-level differences affect differential survival or reproduction, colony-level properties can become relevant to evolutionary change (Okasha, 2006). The existence of selection among colonies, however, does not by itself establish that colonies constitute fully integrated evolutionary individuals. The distribution of heritable

variation, reproductive organization, conflict, and fitness effects across organizational levels remains decisive for that assessment.

Reproductive specialization is particularly significant because it can link the evolutionary fate of non-reproductive colony members to reproduction occurring through other members of the colony. In systems with pronounced reproductive division of labour, the propagation of genes and socially organized traits may depend upon the persistence and reproductive performance of colony-level organization. This provides a stronger basis for considering colony-level Evolutionary Continuity than collective coordination alone.

Colony reproduction nevertheless requires careful distinction from the reproduction of individual insects. New colonies may be established through different processes, including independent founding by reproductive individuals, swarming, budding, or colony fission, depending on the species. These processes generate continuity between successive colony organizations without implying that all eusocial colonies reproduce in the same manner or that every colony-level characteristic is inherited as a collective trait.

Eusociality has played an important role in discussions of evolutionary transitions and the emergence of higher-level individuality (Maynard Smith & Szathmáry, 1995; Okasha, 2006). Such comparisons are most informative when they identify the conditions under which lower-level organisms become sufficiently integrated for selection and reproduction to acquire significant collective organization. They should not be taken to imply that eusociality as such automatically constitutes a completed transition to a new biological individual.

Evolutionary Continuity at colony level is strongest where reproductive specialization, sufficiently aligned fitness interests, differential colony persistence or reproduction, and heritable variation in colony-level organization occur together. These conditions occur to different degrees among eusocial systems.
Evolutionary Continuity can contribute substantially to the case for colony-level biological individuality without determining that attribution independently of the other organizational dimensions.

## 8.6 Adaptive Persistence

Eusocial colonies persist in environments in which resource availability, climatic conditions, predation pressure, colony composition, and other biological circumstances continually change. Colony persistence depends not only upon maintaining existing patterns of organization, but also upon modifying collective activity as conditions change.

Division of labour provides one mechanism through which such adjustment can occur. Task allocation in many eusocial insects is flexible rather than permanently fixed. Changes in colony composition or local conditions can alter the distribution of workers among foraging, brood care, nest maintenance, defense, and other activities. Individual responses to local cues can thereby contribute to changes in colony-level activity without requiring centralized control (Robinson, 1992; Seeley, 2010).

Collective regulation can also involve changes in resource acquisition, recruitment, nest maintenance, defense, and local environmental conditions. The mechanisms and extent of such regulation differ substantially among eusocial taxa. In well-studied honeybee colonies, for example, distributed communication and recruitment allow foraging activity and collective decisions to change in response to available resources and other environmental conditions (Seeley, 2010). Other eusocial systems achieve comparable organizational adjustment through different behavioral, chemical, or spatial mechanisms (Hölldobler & Wilson, 2009).

Adaptive Persistence at colony level can also involve compensation for changes among participating organisms. Workers die, emerge, change behavioral roles, or become unavailable, while colony activities may continue through redistribution of tasks among remaining or newly recruited individuals. The persistence of colony organization need not depend upon the continued participation of particular workers.

These processes should be distinguished from evolutionary adaptation. Changes in task allocation, foraging, defense, or other colony activities can contribute to continued viability within the lifetime of a colony without requiring heritable change across generations. Adaptive Persistence, as used here, concerns the regulated maintenance or restoration of viable organization under changing conditions; evolutionary change is addressed separately through Evolutionary Continuity.

Eusocial colonies can exhibit Adaptive Persistence at the collective level where distributed behavioral and regulatory responses modify colony activity in ways that maintain viable organizational continuity. The extent of this capacity varies among species, colony stages, and environmental conditions. Its presence contributes to colony-level organization without independently establishing colony-level biological individuality.

## 8.7 Ecological Coupling

Eusocial colonies are continuously coupled to their ecological surroundings through flows of resources, energy, organisms, and information. Food acquisition, nest construction, brood production, waste removal, defense, and reproduction all depend upon relations extending beyond the colony itself. Colony organization develops and persists through continuing interaction with environmental conditions rather than through organizational isolation.

Foraging provides a particularly visible expression of this coupling. Colony members move between the nest and surrounding resource environments, and changes in resource distribution can alter recruitment, task allocation, and patterns of collective activity. In well-studied honeybee colonies, communication among foragers allows colony-level foraging activity to respond dynamically to changing distributions of floral resources (Seeley, 2010). Comparable forms of environment-dependent coordination occur through different mechanisms in other eusocial insects (Hölldobler & Wilson, 2009).

The relation between colony and environment can also be reciprocal. Many eusocial insects construct or modify nests that alter temperature, humidity, ventilation, accessibility, and other local conditions relevant to colony persistence. Such environmental modification does not

remove ecological dependence. It changes some of the conditions through which colony organization remains coupled to its surroundings.

Ecological Coupling also includes relations with other organisms. Predators, parasites, pathogens, competitors, prey, food plants, and mutualistic partners can affect colony organization and persistence. The biological significance of these relations varies among eusocial systems, and some may become highly consequential for particular colonies or species. Their importance does not by itself make the participating external organisms components of the colony.

This distinction is essential for separating Ecological Coupling from Organizational Boundaries. A relation may be necessary for colony persistence while remaining a relation between the colony and its ecological Context. Conversely, colony members can move extensively through the environment while continuing to participate in colony organization. Ecological dependence and organizational membership describe different aspects of the colony–environment relation.

Ecological Coupling in eusocial colonies is extensive and dynamically organized, but its configuration varies with species, colony state, habitat, and ecological conditions. It contributes to the maintenance and reorganization of colony-level organization while leaving open the question whether that organization constitutes a biological individual.
That question depends upon its relation to the other organizational dimensions.

## 8.8 Organizational Profile

The preceding analysis shows that eusocial colonies display all six organizational dimensions identified in Chapter 4, although these dimensions are realized through processes distributed across multiple organismal individuals. Their configuration can be summarized as follows.

| **Organizational Dimension** | **Configuration in Eusocial Colonies** |
|---|---|
| Organizational Boundaries | Colony organization is differentiated from its surroundings through a combination of spatial organization, recognition systems, communication, and regulated participation. Colony boundaries remain open and dynamic and do not coincide simply with the physical limits of the nest or the anatomical boundaries of individual insects. |
| Organizational Integration | Division of labour, communication, reproductive specialization, and distributed behavioral regulation coordinate the activities of colony members while the participating insects retain their own physiological and behavioral organization. |
| Adaptive Persistence | Task allocation and other collective activities can be reorganized in response to changes in colony composition and environmental conditions, allowing colony organization to continue despite turnover among individual members and changing circumstances. |
| Developmental Continuity | Colony organization can persist through successive changes in demographic composition, brood development, caste differentiation, and incorporation of new members. Continuity within a colony remains distinct from reproduction and continuity between successive colonies. |
| Ecological Coupling | Colony organization depends upon continuing exchanges with its ecological surroundings through resource acquisition, environmental modification, and interactions with other organisms. Ecological dependence does not by itself determine organizational membership. |
| Evolutionary Continuity | Reproductive division of labour can connect the evolutionary fate of non-reproductive members to colony reproduction. Colony-level evolutionary continuity is strongest where reproductive specialization, aligned fitness interests, differential colony persistence or reproduction, and heritable variation in colony-level organization occur together. |

This profile differs from those of the preceding cases in an important respect. In eusocial colonies, several organizational dimensions can become strongly coordinated at the collective

level while the constituent organisms remain biologically organized individuals. Colony organization provides a particularly informative case for examining whether biological individuality can occur at more than one organizational level.

The profile itself does not resolve that question. The presence of all six dimensions is not being proposed as a sufficient criterion for biological individuality, nor has the comparative framework established a threshold at which their convergence becomes constitutive of individuality. The profile instead identifies the organizational configuration that must be evaluated in relation to the cell, biofilm, and holobiont cases.

## 8.9 Evaluation

Eusocial insect colonies present a distinctive configuration of the six organizational dimensions examined in this monograph. Organizational Integration can extend across large numbers of multicellular organisms through division of labour, communication, reproductive specialization, and distributed regulation. Organizational Boundaries can be maintained through spatial organization, recognition systems, and regulated participation, while Adaptive Persistence allows collective activity to be reorganized as colony composition and environmental conditions change. Developmental Continuity extends across turnover among colony members, Ecological Coupling connects colony organization continuously to its surroundings, and Evolutionary Continuity can acquire a collective dimension where reproductive specialization, aligned fitness interests, colony reproduction, and heritable colony-level variation occur together.

This organization distinguishes eusocial colonies from a simple aggregation of social organisms. Colony-level organization can persist beyond the participation of particular workers, coordinate differentiated activities, regulate relations between members and surroundings, and contribute directly to survival and reproduction. These properties justify treating the colony as a genuine level of biological organization rather than merely as a convenient descriptive grouping.

The existence of colony-level organization does not, however, resolve the question of colony-level biological individuality. The constituent insects remain biological organisms with their own boundaries, physiological organization, developmental trajectories, and, depending on species and caste, differing reproductive capacities. Colony organization is realized through relations among entities that already possess substantial organismal individuality.

Evolutionary organization is especially important in evaluating this case. Reproductive specialization and the alignment of fitness interests can make colony persistence and reproduction increasingly consequential for the evolutionary fate of colony members. Yet these conditions vary substantially among eusocial systems, as do reproductive conflict, modes of colony founding, degrees of caste specialization, and the heritability of colony-level characteristics. Eusociality alone does not establish a uniform level of colony individuality.

The comparison also shows why no single organizational dimension can determine the result. Extensive Organizational Integration does not by itself establish individuality; neither do a regulated boundary, long-term persistence, ecological interdependence, developmental continuity, or colony-level evolutionary effects considered separately. What matters for the

present analysis is how these dimensions are configured and related within particular biological systems.

Eusocial colonies provide a strong case for distinguishing collective biological organization from the stronger attribution of collective biological individuality. The analysis supports the former directly. The latter remains a comparative question whose answer depends upon how the six organizational dimensions are configured and related at colony level while remaining distributed across organismal individuals.

The eusocial case extends the comparative sequence without resolving it prematurely. Cells, biofilms, holobionts, and eusocial colonies each display persistent biological organization, but they distribute boundaries, integration, adaptive regulation, developmental continuity, ecological relations, and evolutionary continuity differently across organizational levels.
The significance of these differences for a relational account of biological individuality can now be examined comparatively in Chapter 9.

# Part IV – Comparative Analysis

## Chapter 9. Comparative Organizational Analysis

### 9.1 Introduction

The preceding chapters examined four biologically different forms of organization: the free-living cell, the biofilm, the holobiont, and the eusocial insect colony. Each case was analyzed through the six dimensions introduced in Chapter 4: Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity.

The purpose of the comparison is now to determine what this common analytical framework reveals about the organization of biological individuality. Because the same dimensions were deliberately applied to all four cases, their presence across the case studies cannot itself be treated as an independent empirical finding. The relevant comparison lies instead in how these dimensions are biologically realized, how they relate to one another, and where their configurations converge or diverge across organizational levels.

The cases already indicate substantial differences. In the cellular reference case, several dimensions are closely integrated within a physically bounded living system. Biofilms distribute collective organization across interacting microbial cells and extracellular structures without necessarily integrating all dimensions at the collective level. Holobionts reveal how extensive functional and ecological relations can connect organisms from different evolutionary lineages while leaving organizational membership and evolutionary individuality contested. Eusocial colonies show how division of labour, communication, reproductive specialization, and collective regulation can generate persistent organization among multicellular organisms that remain biological individuals in their own right.

These differences make comparison more informative than a search for a single defining property. Biological systems can display boundaries, integration, adaptive regulation, developmental continuity, ecological coupling, and evolutionary continuity in different combinations and through different mechanisms. The question is whether particular relations among these dimensions help explain why biological individuality appears comparatively clear in some cases and more difficult to attribute in others.

This comparison also provides an initial test of a broader proposition developed within the PSE Research Programme: that recurrent forms of organization may occur across different biological scales. Such recurrence cannot be inferred merely from applying the same conceptual vocabulary to different cases. Evidence for Organizational Scale Invariance would require identifiable organizational relations that recur despite differences in material realization and scale, together with criteria by which genuine recurrence can be distinguished from similarities introduced by the analytical framework itself.

Chapter 9 has two related aims. The first is comparative: to identify similarities and differences in the organization of the four biological cases without presupposing that they instantiate a single form of individuality. The second is theoretical: to determine what, if anything, this comparison

contributes to the PSE hypotheses concerning Persistent Organization, Biological Individuality, and Organizational Scale Invariance.

## 9.2 Comparative Organizational Profiles

The organizational profiles developed in Chapters 5–8 allow the four cases to be compared without reducing their differences to numerical or ordinal scores. Each case displays the six dimensions introduced in Chapter 4, but the biological processes through which those dimensions are realized, and the organizational levels at which they become integrated, differ substantially.

**Table 9.1. Comparative organizational profiles of the four biological cases**

| Organizational Dimension | Free-Living Cell | Biofilm | Holobiont | Eusocial Insect Colony |
|---|---|---|---|---|
| **Organizational Boundaries** | Membrane-based boundary regulates exchange while maintaining cellular organization as a distinguishable unit. | Collective boundary is diffuse and dynamic, involving cells, extracellular matrix, spatial structure, and interfaces with the surrounding environment. | Host boundaries, microbial distributions, and immune and physiological processes overlap without necessarily defining a single boundary of collective membership. | Spatial organization, recognition systems, communication, and regulated participation contribute to a colony boundary that does not coincide simply with the nest or with organismal boundaries. |
| **Organizational Integration** | Metabolic, regulatory, structural, and informational processes are coordinated within one cellular system. | Cells can become collectively integrated through extracellular matrix, spatial gradients, signalling, metabolic interactions, and other local relations, with substantial variation among biofilms. | Host and microbial processes can become functionally interconnected while participating organisms retain distinct physiological and evolutionary organization. | Division of labour, communication, reproductive specialization, and distributed regulation coordinate multiple organismal individuals while those individuals retain their own biological organization. |
| **Adaptive Persistence** | Regulatory processes maintain or restore viable cellular organization as internal and external conditions change. | Collective organization can respond to changing conditions through physiological regulation, altered gene expression, spatial reorganization, and changes in community activity. | Host and microbial components can change in composition and activity while functionally important host–microbiome relations persist or reorganize. | Task allocation and other collective activities can be reorganized in response to changing colony composition and environmental conditions. |
| **Developmental Continuity** | Cellular continuity persists through regulated growth and maintenance within the lifetime of the cell; reproduction generates successor cells and must be distinguished from persistence of the same cell. | Biofilms can undergo temporally structured formation, growth, reorganization, and dispersal, but these processes vary among systems and do not constitute a universal collective developmental programme. | Host development and microbial community assembly interact, but their developmental histories remain only partly coincident and microbial membership can change substantially through time. | Colony organization can persist through brood development, demographic change, caste differentiation, and turnover among members; continuity within a colony remains distinct from reproduction between colonies. |
| **Ecological Coupling** | Cellular viability depends upon continuous material and energetic exchange with the surrounding environment. | Biofilm organization is strongly shaped by substrates, resource gradients, flow conditions, surfaces, and interactions with surrounding organisms and environments. | Host–microbiome organization is constituted through extensive ecological and physiological interactions among host, microorganisms, and wider environment. | Resource acquisition, environmental modification, and interactions with other organisms continuously connect colony organization to its ecological surroundings. |
| **Evolutionary Continuity** | Reproduction and heredity connect cellular lineages across generations, although persistence of an individual cell remains distinct from lineage continuity. | Biofilms can structure selection and generate collective effects without necessarily reproducing as coherent evolutionary units. | Host and microbial partners can have different reproductive histories and evolutionary interests; functional association therefore does not by itself establish a common evolutionary individual. | Reproductive specialization can generate substantial colony-level evolutionary organization where fitness alignment, colony reproduction, and heritable collective variation converge. |

The comparison reveals neither a uniform progression nor a simple hierarchy among the four cases. The free-living cell shows close coordination of several dimensions within a single physically bounded system, but its persistence as an individual cell must still be distinguished from reproductive and lineage continuity. Biofilms show that substantial collective integration and adaptive regulation can occur while boundaries, developmental continuity, and evolutionary continuity remain comparatively distributed or variable. Holobionts show particularly clearly that functional and ecological interdependence need not coincide with common organizational membership or evolutionary individuality. Eusocial colonies show that extensive collective integration, developmental continuity, and reproductive specialization can arise among organisms that retain substantial individuality at the organismal level.

The comparison shifts attention from the presence or absence of isolated properties to relations among the six dimensions. In some systems several dimensions are closely coordinated at the same organizational level; in others they are distributed across components, temporal processes, or evolutionary lineages. The attribution of biological individuality becomes more difficult where these organizational relations are distributed across different organizational levels.

Table 9.1 should be read as a comparative map of organizational configurations, not as a scale of increasing individuality. It does not establish a threshold above which a system becomes a biological individual, nor does it imply that all six dimensions contribute equally in every biological case. Its purpose is to make the patterns of convergence and divergence identified in the four case studies available for further analysis.

## 9.3 Recurring Organizational Relations

The comparison in Table 9.1 reveals recurring relations among organizational dimensions, but these recurrences require careful interpretation. Because the six dimensions were selected in advance as a common analytical framework, their repeated identification across the four cases does not demonstrate that they constitute universal principles of biological organization. More informative are the ways in which particular dimensions interact, converge, or remain separated in biologically different systems.

One recurring relation concerns boundaries and integration. In each case, persistent biological organization involves some regulation of interactions between participating processes and their surroundings. The mechanisms differ substantially: membrane-mediated exchange in cells, spatial and extracellular organization in biofilms, overlapping host and microbial interfaces in holobionts, and recognition-mediated and behavioral relations in eusocial colonies. Organizational Integration likewise takes different forms, ranging from intracellular coordination to relations among physiologically autonomous organisms. The comparison identifies a recurring relation between differentiation from surroundings and internal coordination without implying a common physical boundary mechanism.

A second relation concerns persistence and regulated change. None of the cases persists through complete invariance of its components or activities. Cells continually exchange matter and regulate internal processes; biofilms can reorganize cellular activity and spatial structure; host–microbiome associations change in composition and function; and eusocial colonies undergo continual turnover and redistribution of activity among their members. Persistent biological organization is compatible with substantial internal change where relevant organizational relations continue or are reorganized under changing conditions.

A third relation concerns the separation of organizational timescales. Persistence of an existing organization, developmental continuity, reproduction, and evolutionary lineage continuity are related but distinct processes. The distinction is comparatively clear in the cellular case and becomes increasingly important in collective systems, where participating organisms and collective organization may have different developmental and reproductive histories. The same biological system can display continuity at one organizational level while undergoing replacement, reproduction, or evolutionary change at another.

The cases also reveal a recurring distinction between ecological dependence and organizational membership. Every biological organization examined here depends upon relations extending beyond its boundaries, but dependence alone does not determine which entities or processes belong to the organization under consideration. This issue is particularly visible in holobionts and eusocial colonies, where biologically consequential interactions can extend across multiple organisms and into the surrounding environment. Ecological Coupling and Organizational Boundaries must therefore remain analytically distinct even where they are causally interdependent.

Finally, the comparison shows that organizational dimensions need not converge at the same biological level. In the free-living cell, several dimensions are closely coordinated within a single cellular organization. In biofilms, holobionts, and eusocial colonies, some dimensions can acquire collective organization while others remain distributed across constituent organisms, ecological relations, or evolutionary lineages. The resulting configurations help explain why attribution of biological individuality becomes less straightforward in collective systems.

These recurring relations are more limited claims than a general principle of organizational invariance. They identify comparative patterns generated by the four case studies while leaving open whether the same relations recur in other biological systems, at other organizational scales, or outside biology. Establishing such recurrence would require independent cases and criteria capable of distinguishing genuine structural correspondence from similarities produced by the analytical framework.

The comparison provides a basis for examining a broader PSE hypothesis of Organizational Scale Invariance, without yet confirming it. The question is whether relations of differentiation, constraint, integration, selective persistence, and organizational continuity recur across scales in forms that are structurally comparable despite differences in their material realization. That hypothesis is examined in the following section.

## 9.4 Organizational Scale Invariance

Organizational Scale Invariance is the PSE hypothesis that comparable organizational relations can recur at different scales despite substantial differences in the entities, mechanisms, and material processes through which they are realized. The claim concerns organizational architecture, not physical similarity between systems and not the recurrence of any particular biological mechanism.

The four cases examined here provide a limited biological setting in which this hypothesis can be explored. Cells, biofilms, holobionts, and eusocial colonies differ greatly in composition, spatial organization, developmental history, ecological relations, and evolutionary structure. The comparative analysis nevertheless identifies relations involving differentiation from surroundings, selective interaction, integration, persistence through change, and continuity across time. These relations are realized differently in each case and do not necessarily converge at the same organizational level.

Such similarities are suggestive, but they do not by themselves establish Organizational Scale Invariance. The six dimensions used in the comparison were selected in advance, and the cases were subsequently analyzed through that framework. Recurrence of the analytical categories is therefore partly a consequence of the research design. Evidence for scale invariance would require a stronger result: structurally comparable organizational relations should be identifiable independently of the terminology used to describe them and should generate explanatory or empirical consequences that are not produced merely by applying the same conceptual scheme.

This requirement distinguishes Organizational Scale Invariance from the more general observation that complex systems can display recurrent quantitative or structural regularities across scales. Complexity science has documented many such regularities, including scaling relations, network structures, feedback processes, and patterns of self-organization in systems with very different material realizations (Mitchell, 2009). These findings establish the scientific importance of cross-scale regularities, but they do not establish the specifically PSE claim that such recurrence reflects a common ontological architecture of organization.

The PSE hypothesis proposes a more specific explanatory sequence. As developed in Ontology of Organization (Monograph No. 2), organization is analyzed through relations among Context, Distinction, Systematic Exclusion, Boundary, Constraint, Selective Persistence, Coherence, Persistent Organization, and Identity (Stolting, 2026c). Organizational Scale Invariance would occur where this relational architecture, or a theoretically specified part of it, can be shown to recur across organizational levels while being realized through different domain-specific mechanisms.

The biological cases in this monograph provide partial grounds for investigating that possibility. Membranes, extracellular matrices, immune and physiological interactions, nest mate-recognition systems, metabolic regulation, microbial interactions, and social communication are biologically different mechanisms. Their roles can nevertheless be compared in terms of how they regulate interactions, contribute to organizational differentiation, and participate in the persistence of organized systems. The comparison becomes relevant to Organizational Scale Invariance only where such functional similarities can be related to the same underlying organizational relations without erasing the biological differences among the cases.

A stronger test would require independent operationalization. The hypothesis should specify which relations are expected to recur, how their presence can be identified without presupposing the PSE vocabulary, and what observations would count against the proposed correspondence. It should also distinguish genuine cross-scale recurrence from superficial analogy, convergent terminology, and similarities introduced by the investigator. Comparative extension to additional biological systems would then provide a more demanding test of whether the proposed architecture has explanatory reach beyond the cases from which it was developed.

Organizational Scale Invariance should be treated here as a research hypothesis supported by a developing comparative programme, not as a result demonstrated by the four case studies. The comparative analysis identifies candidate organizational correspondences and clarifies the conditions under which they could become evidentially significant. Whether those

correspondences constitute a genuinely scale-invariant organizational architecture remains open to further comparative and empirical investigation.

## 9.5 Biological Individuality Reconsidered

The comparative analysis supports a relational account of biological individuality while also showing why Persistent Organization alone cannot provide a sufficient criterion. Cells, biofilms, holobionts, and eusocial colonies can all sustain forms of persistent organization, yet the six biological dimensions examined in Chapters 5–8 are configured differently in each case. Biological individuality requires analysis of how persistent organization is biologically realized and how its organizational dimensions are related at the level under consideration.

The free-living cell provides the clearest reference case in this comparison. Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity are closely related through a cellular organization whose identity can persist through substantial material and functional change. Even here, however, persistence of an individual cell must be distinguished from cell reproduction and from continuity of the evolutionary lineage to which it belongs.

The collective cases make this distinction more consequential. Biofilms can exhibit substantial collective integration and adaptive persistence while their boundaries, developmental continuity, and evolutionary continuity remain variable or distributed. Holobionts can involve extensive physiological and ecological interdependence without requiring host and microbial lineages to constitute a single evolutionary individual. Eusocial colonies can develop highly organized division of labour, boundary regulation, adaptive responses, developmental continuity, and reproductive specialization while their constituent insects remain biological individuals.

Biological individuality cannot be inferred from integration, persistence, dependence, or evolutionary relevance considered separately. Nor does the presence of all six analytical dimensions establish individuality by itself. The comparative question concerns whether these dimensions form a sufficiently integrated biological organization at the level under consideration, while remaining distinguishable from relations that primarily belong to constituent organisms, ecological Context, or broader evolutionary lineages.

This formulation also avoids treating individuality as necessarily confined to a single privileged scale. The case studies show that biologically consequential organization can occur simultaneously at cellular, organismal, collective, and ecological levels. Whether more than one of these levels should be attributed biological individuality is an empirical and theoretical question for particular systems. The existence of organization at multiple levels establishes the possibility of nested organization; it does not by itself establish nested individuality.

A relational account shifts the question from identifying a universal material property possessed by every biological individual to examining the organization through which biological continuity is maintained. Boundaries, integration, adaptive regulation, development, ecological coupling, and evolutionary continuity become relevant through their relations within a particular biological

organization. Their relative importance and relations within the larger organization may differ among biological systems.

This leaves an important question unresolved. The comparative framework can identify configurations associated with clearer and more contested cases of biological individuality, but it has not yet established a necessary and sufficient combination of organizational dimensions or an independently validated threshold of convergence. The framework should therefore be understood as a means of analyzing biological individuality and generating comparative hypotheses, rather than as a completed criterion for deciding every disputed case.

Biological individuality, on this account, is best investigated through the biologically specific configuration of Persistent Organization, including its boundaries, integration, adaptive persistence, developmental continuity, ecological coupling, and evolutionary continuity. Determining when such coordination warrants the stronger attribution of individuality remains a biological question that must be resolved through comparative and empirical investigation.

## 9.6 Scope and Future Applications

The comparative analysis developed in this monograph is deliberately limited in scope. Four cases were selected to represent different configurations of biological organization: a free-living cell, a biofilm, a holobiont, and a eusocial insect colony. These cases provide substantial contrasts in material composition, spatial organization, developmental continuity, ecological relations, and evolutionary structure, but they do not represent the full diversity of biological individuality.

The six-dimensional framework can be extended to additional biological systems, but such extension should serve as a test rather than merely as an application of the framework. Candidate cases include multicellular organisms, modular organisms, clonal colonies, fungal networks, colonial marine organisms, symbiotic associations, and other systems in which the location or continuity of biological individuality is contested.
The relevant question is not simply whether Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity can be described in each case, but *whether their configurations reveal reproducible relations that distinguish clearer from more contested forms of biological individuality*.

Comparative extension also requires cases that challenge the framework. Systems should be sought in which persistent biological organization occurs despite weak convergence among the six dimensions, as well as cases in which several dimensions appear strongly integrated without yielding a compelling attribution of individuality. Such cases would help determine whether the dimensions identify biologically informative relations or merely provide a flexible vocabulary capable of accommodating almost any organized biological system.

A stronger empirical programme would require operational criteria for each dimension. Organizational Boundaries would need observable indicators of regulated membership or interaction; Organizational Integration, indicators of functional dependence and coordination; Adaptive Persistence, measures of regulated organizational response under changing

conditions; Developmental Continuity, criteria distinguishing persistence from reproduction and succession; Ecological Coupling, measures of organism–environment dependence and reciprocal interaction; and Evolutionary Continuity, evidence concerning reproduction, heredity, differential fitness, and the distribution of selection across organizational levels. The appropriate indicators will differ among biological systems, but their relation to each analytical dimension should be specified independently of the outcome concerning individuality.

The same requirement applies to *Organizational Scale Invariance*. Further cases would support that hypothesis only if structurally comparable organizational relations could be identified across scales independently of the repeated use of PSE terminology.
A stronger test would specify in advance which relations are expected to recur, which domain-specific differences are compatible with the proposed correspondence, and which observations would count against it. Failure to identify the predicted relations in appropriate comparison cases would then constrain the scope of the hypothesis rather than being absorbed through reinterpretation.

Future work should also compare the organizational framework with established approaches to biological individuality. Evolutionary, physiological, immunological, developmental, ecological, and information-based accounts identify different processes as relevant to individuality. The purpose of such comparison would be to determine whether the relational framework integrates distinctions already recognized in those approaches, generates additional explanatory consequences, or merely redescribes them in different terminology.
The latter possibility must remain an explicit critical alternative.

The framework developed here should therefore be treated as a comparative research instrument whose explanatory value depends upon its performance beyond the cases used in its construction. Its strongest future applications will be those that expose it to biological systems capable of differentiating between competing interpretations, revealing limits to its applicability, or generating predictions that can be investigated independently.

## 9.7 Conclusion

The comparative analysis of cells, biofilms, holobionts, and eusocial insect colonies shows that biological organization can persist through markedly different configurations of boundaries, integration, adaptive regulation, developmental continuity, ecological coupling, and evolutionary continuity. These dimensions do not necessarily coincide at the same organizational level, nor do they contribute in identical ways to the persistence and identity of the systems examined.

This variation clarifies the relation between Persistent Organization and Biological Individuality. Persistent Organization provides an ontological basis for analyzing continuity through change, but its presence alone does not establish biological individuality. The biological question concerns how organizational continuity is realized through specifically biological processes and how the six dimensions are configured and coordinated at the level under consideration.

The collective cases make this distinction particularly clear. Biofilms, holobionts, and eusocial colonies can display substantial organization beyond the level of their constituent organisms without thereby requiring attribution of collective biological individuality.
Collective organization and collective individuality must therefore remain analytically distinct. At the same time, the persistence of organization across turnover of components shows that biological identity cannot be reduced simply to the continued presence of particular material constituents.

Comparison across the four cases also identifies candidate recurring organizational relations. Differentiation from surroundings is associated with regulated interaction and integration; persistence involves both continuity and regulated change; developmental, reproductive, and evolutionary continuity operate on distinguishable timescales; and ecological dependence does not by itself determine organizational membership.
These relations provide comparative results that can be investigated in additional biological systems.

Their recurrence does not yet demonstrate Organizational Scale Invariance. Because the cases were analyzed through a common conceptual framework, stronger evidence would require independent operationalization, additional comparison cases, and criteria capable of distinguishing genuine structural recurrence from similarities introduced by the framework itself. Organizational Scale Invariance therefore remains a PSE research hypothesis whose scope and explanatory significance require further testing.

The comparative analysis supports a relational investigation of biological individuality while leaving the stronger ontological implications open to further examination. It establishes neither a universal definition of the biological individual nor a threshold at which Persistent Organization becomes individuality.
Instead, it provides a structured basis for examining how biological identity can be maintained across material change, component turnover, ecological interaction, development, and evolutionary continuity.

Chapter 10 develops the ontological implications of these findings. Its task is not to convert the comparative framework into a completed theory of biological individuality, but to determine what kind of relational ontology can be justified by the distinctions and limitations established in the preceding analysis.

# Part V — Synthesis

## Chapter 10. Toward a Relational Ontology of Biological Individuality

### 10.1 Beyond Essentialist Definitions

Biological individuality has been approached through a wide range of criteria, including physiological integration, developmental unity, immunological boundaries, reproduction, genetic homogeneity, evolutionary interests, and ecological interaction. Each captures biologically important aspects of individuality, yet none applies without qualification across the diversity of systems considered in contemporary biology (Godfrey-Smith, 2009; Pradeu, 2012; Clarke, 2013).

The comparative analysis in this monograph helps explain why. Cells, biofilms, holobionts, and eusocial insect colonies do not differ merely in the degree to which they possess a common defining property. They differ in how Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity are realized and in the organizational levels at which these dimensions coincide or remain distributed.

This suggests that biological individuality is unlikely to be captured adequately by identifying a single intrinsic property of an entity. Anatomical boundaries, physiological processes, genetic relations, developmental histories, and reproductive capacities remain biologically important, but their significance for individuality depends upon how they participate in the organization and continuity of the biological system under consideration.
A relational approach does not replace biological properties with relations; it examines how properties, processes, and relations jointly contribute to persistent biological organization.

The collective cases make this especially clear. A biofilm can display coordinated collective activity without possessing the developmental or evolutionary continuity characteristic of a paradigmatic organism. A host and its microbiota can be physiologically and ecologically interdependent while retaining partly distinct organizational and evolutionary histories. A eusocial colony can sustain extensive division of labour and reproductive specialization while its constituent insects remain organisms with their own physiological and developmental organization.
In each case, the attribution of individuality depends upon how biological continuity is distributed across organizational levels.

Biological individuality should therefore be approached as a problem of organizational configuration rather than as the possession of one universally decisive characteristic. The six dimensions used in this monograph provide a comparative framework for analyzing such configurations; they are not proposed as necessary and sufficient criteria. Their value lies in making explicit where different forms of biological continuity converge, where they remain separate, and how those relations affect the attribution of individuality.

This position also preserves an important distinction established in the preceding chapters. *Persistent Organization is broader than Biological Individuality*. A system may maintain an identifiable organization through changing components and conditions without thereby constituting a biological individual. The ontological concept of Persistent Organization can provide a basis for analyzing biological continuity, while the attribution of Biological Individuality requires additional biological analysis.

A relational ontology of biological individuality begins from this distinction. Its task is to explain how biological identity can remain identifiable through material turnover, developmental change, ecological interaction, and evolutionary continuity without reducing individuality either to material sameness or to any single biological criterion.
The following sections examine how far the PSE concept of Persistent Organization can contribute to such an account and where further biological specification remains necessary.

## 10.2 A Relational Ontology of Persistent Organization

Persistent Organization was introduced in Monograph No. 2 as a domain-independent ontological concept. It refers to organization whose identity remains distinguishable through change as relevant relations, constraints, and processes continue or are reorganized while organizational continuity is maintained.
The concept does not presuppose biological individuality and is not restricted to living systems.

This distinction is essential for the analysis developed here. Biological systems are materially realized organizations: cells require membranes, molecular structures, metabolic processes, and material and energetic exchange; biofilms depend upon microbial cells, extracellular structures, and local physicochemical conditions; holobionts involve interacting organisms and physiological processes; and eusocial colonies depend upon the bodies, activities, and relations of their constituent organisms.
A relational ontology does not detach organization from these material realizations. It asks how their changing components and processes remain organized as an identifiable system through time.

Persistence therefore does not require material identity. Biological components are continually replaced, transformed, produced, or lost. What remains identifiable is an organization in which relevant relations and constraints continue, or are reorganized, without loss of organizational identity. The material realization matters because changes that disrupt the relations required for that organization can also terminate its persistence.

This makes Context indispensable. Organizational persistence is always persistence under particular conditions and through particular relations with surroundings. A configuration may remain internally coherent while changing environmental conditions undermine the relations required for its continued persistence. Persistence may also fail when regulatory processes required for organizational continuity are disrupted. Persistent Organization is relational both internally, through relations among participating processes, and externally, through the conditions under which those relations can continue.

In biological systems, this general ontology acquires domain-specific realization. Organizational Boundaries regulate relations between biological organization and surroundings; Organizational Integration coordinates participating processes; Adaptive Persistence concerns continued viability through regulated change; Developmental Continuity connects organizational states through biological time; Ecological Coupling situates organization within continuing organism–environment relations; and Evolutionary Continuity concerns reproduction, heredity, differential reproductive success, and change across generations.
These dimensions specify biologically relevant forms of continuity without redefining the underlying concept of Persistent Organization.

Persistent biological organization can be understood as a biological realization of the more general ontological architecture developed in the PSE Research Programme.
This does not imply that every persistent biological organization constitutes a biological individual. Biofilms, holobionts, and eusocial colonies demonstrate why the distinction matters: persistent organization can occur collectively even where boundaries, developmental histories, reproductive organization, and evolutionary continuity remain distributed across participating biological entities.

The contribution of Persistent Organization to a relational ontology of biological individuality is consequently foundational but limited. It explains how organizational identity can remain distinguishable through material and relational change.
Whether such persistence constitutes the continuity of a biological individual depends upon additional biological organization and cannot be decided by the ontological concept alone.

## 10.3 Persistent Organization within the PSE Ontology

Persistent Organization occupies a specific position within the ontology developed by the PSE Research Programme. Systematic Exclusion is the proposed generative organizational principle; Persistent Organization describes an organizational condition that can arise where selective relations, boundaries, and constraints contribute to the continuation of an identifiable organization through change.
The two concepts should therefore not be treated as equivalent ontological principles.

The relevant conceptual sequence can be expressed as:

Context → Distinction → Systematic Exclusion → Boundary → Constraint → Selective Persistence → Coherence → Persistent Organization → Identity

This sequence represents conceptual dependencies rather than a universal temporal progression. Context specifies the relational domain within which distinctions become organizationally consequential. Systematic Exclusion concerns the selective organization of possibilities within that Context. Boundaries and constraints regulate relations through which some organizational configurations persist while alternatives do not. Selective Persistence and Coherence describe further conditions relevant to the continuation of identifiable organization, while Persistent Organization and organizational Identity remain analytically distinguishable concepts.

Biological systems provide domain-specific realizations of this architecture. A cellular membrane regulates molecular exchange; biofilm organization depends upon selective interactions among cells, extracellular structures, and surroundings; host–microbiome relations are mediated through physiological, ecological, and immune processes; and eusocial colonies regulate interaction and participation through communication, recognition, division of labour, and reproductive organization.
These mechanisms are biologically different and should not be treated as interchangeable manifestations of a single physical process.

Their relevance to PSE lies in a more limited structural question: *whether these different mechanisms instantiate comparable organizational relations involving differentiation, constraint, selective interaction, and persistence*.
The comparative analyses in this monograph identify candidate correspondences of this kind. They do not establish that every mechanism examined is generated by Systematic Exclusion in the same empirical sense, nor that the recurrence of PSE terminology demonstrates a common underlying architecture.

The distinction between material and organizational continuity remains important within this account. Biological systems continually exchange, replace, produce, and lose material components. Organizational persistence concerns the continuation or reorganization of relations required for an identifiable organization through such change. Material processes remain constitutive of the biological realization, while organizational identity need not depend upon the continued presence of the same material constituents.

Persistent Organization provides an ontological bridge between the domain-independent PSE architecture and the biological analysis developed in this monograph. It allows biological continuity to be examined without reducing identity to material sameness.
Its explanatory contribution remains distinct from the stronger attribution of Biological Individuality, which requires the additional biological analysis represented by Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity.

The biological comparison therefore does not establish Persistent Organization as a second ontological principle. It examines whether a domain-independent organizational concept generated within the PSE ontology can illuminate biologically different forms of continuity and provide a common basis for comparing their organizational configurations. The explanatory scope of that proposal remains subject to the comparative and empirical tests identified in Chapter 9.

## Figure 10.1. From PSE Ontology to the Analysis of Biological Individuality

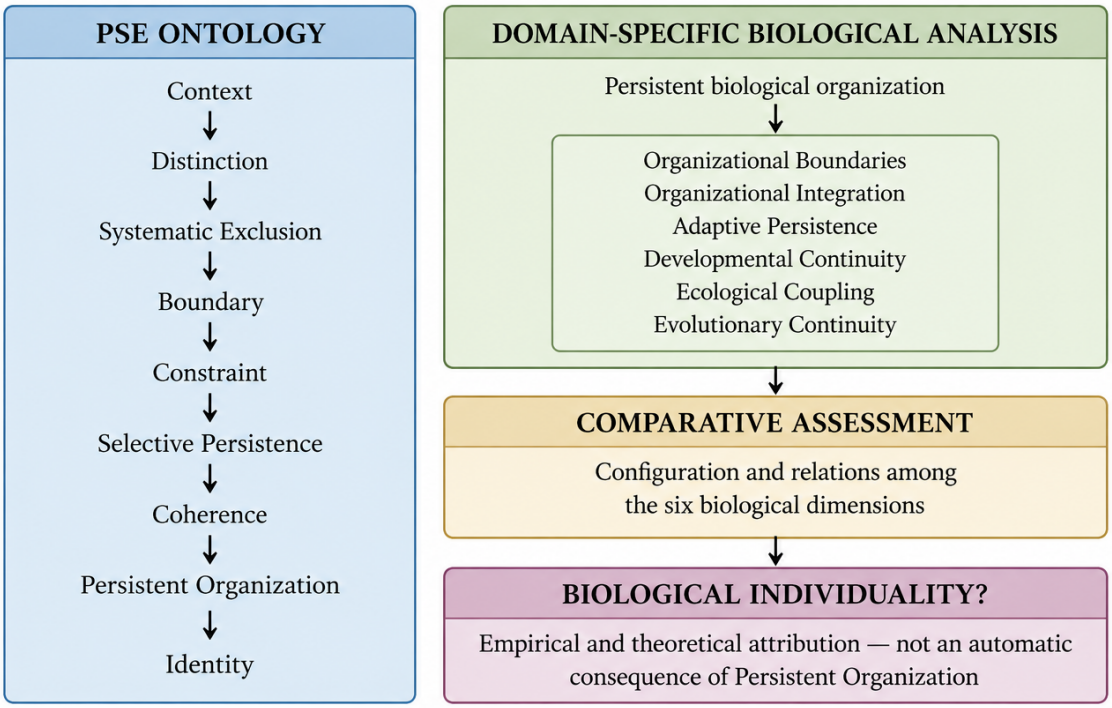



**Figure 10.1. From PSE Ontology to the Analysis of Biological Individuality.** Persistent Organization forms part of the domain-independent organizational architecture developed within the PSE Research Programme. In biological systems, organizational persistence is examined through six domain-specific analytical dimensions: Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity. Their configuration provides the basis for comparative assessment of Biological Individuality.

The figure does not represent Biological Individuality as an automatic consequence of Persistent Organization or of the presence of the six dimensions.

## 10.4 Organizational Scale Invariance

Organizational Scale Invariance extends the PSE analysis beyond the persistence of particular organizations. It proposes that comparable organizational relations may recur at different scales even where the entities, mechanisms, and material processes through which those relations are realized differ substantially (Stolting, 2026b).

This proposition concerns relational architecture rather than material similarity. A cellular membrane, the extracellular organization of a biofilm, physiological and ecological relations within a holobiont, and recognition and communication processes within a eusocial colony are biologically different phenomena. Organizational Scale Invariance would not require these mechanisms to be equivalent. It would require evidence that they participate in structurally comparable relations of differentiation, constraint, selective interaction, integration, and persistence at their respective organizational levels.

If such recurrence can be established independently, its ontological significance would be substantial. It would suggest that organization at different scales can be understood through recurring relational dependencies without requiring a unique organizational principle for each material level.
Domain-specific mechanisms would remain indispensable to biological explanation, while the PSE ontology would address a more general question: *why materially different systems can instantiate comparable forms of persistent organization*.

The comparative analysis in this monograph identifies candidate correspondences of this kind. Cells, biofilms, holobionts, and eusocial colonies all involve regulated relations between organization and surroundings, persistence through changing components and conditions, and forms of integration that contribute to identifiable biological organization. Their mechanisms and the organizational levels at which the six biological dimensions are realized nevertheless differ substantially.

These observations do not establish Organizational Scale Invariance. As argued in Chapter 9, recurrence identified through a common analytical framework may partly reflect the framework itself. The hypothesis therefore requires independent criteria for structural correspondence, comparison with additional and deliberately challenging cases, and specification of observations that would restrict or contradict its proposed scope.

Organizational Scale Invariance should remain distinct from the broader study of scaling and cross-scale regularities in complexity science. Complexity research has documented recurring quantitative and structural patterns across diverse systems (Mitchell, 2009).
Such findings demonstrate that cross-scale regularity is scientifically significant, but they do not establish the specifically PSE proposition that comparable organizational relations reflect a domain-independent ontological architecture.

Within the PSE Research Programme, Organizational Scale Invariance functions as a hypothesis concerning the possible recurrence of organizational architecture across scales. Monograph No. 3 contributes biological comparison cases and candidate correspondences; it does not establish the hypothesis as a general property of living systems. Its broader validity depends

upon comparative and empirical work capable of distinguishing structural recurrence from analogy or conceptual re-description.

## 10.5 Implications for Biological Theory

The relational analysis developed in this monograph has several implications for the study of biological organization. Its principal contribution is not the replacement of established biological accounts of individuality, but the possibility of relating processes usually examined through different theoretical perspectives within a common organizational analysis.

Biological individuality is studied through physiological, developmental, immunological, ecological, and evolutionary approaches, each of which identifies processes relevant to the formation and persistence of biological units. The comparative cases examined here show why these perspectives need not identify the same organizational boundary or the same level of individuality.
Physiological integration may occur among entities with distinct evolutionary histories; ecological dependence may extend beyond organizational membership; developmental continuity may occur at a different level from reproductive continuity; and evolutionary interests may be distributed differently from physiological organization.

The six analytical dimensions developed in Chapter 4 provide a way of preserving these distinctions while examining their relations. Organizational Boundaries concern the regulation of relations between an organization and its surroundings. Organizational Integration concerns coordination among participating processes. Adaptive Persistence concerns the maintenance or restoration of viable organization under changing conditions. Developmental Continuity concerns connected organizational states through biological time. Ecological Coupling concerns continuing relations with the surrounding biological and physical environment. Evolutionary Continuity concerns reproduction, heredity, differential reproductive success, and change across generations.
None of these dimensions can substitute for the biological mechanisms through which it is realized.

This approach has particular relevance to systems in which conventional organismal boundaries become difficult to apply. Biofilms, holobionts, and eusocial colonies show that substantial biological organization can extend beyond the boundaries of a paradigmatic organism. Such organization may involve coordination, mutual dependence, component turnover, environmental regulation, or reproductive specialization without requiring all relevant forms of continuity to coincide at the collective level. Biological theory therefore benefits from distinguishing the existence of collective organization from the stronger attribution of collective individuality.

A second implication concerns biological identity through time. Material turnover does not necessarily terminate an existing biological organization, while reproduction or succession does not necessarily preserve the identity of the same biological individual.
Persistence, development, reproduction, and evolutionary lineage continuity should therefore remain conceptually distinct even where they are causally connected. This distinction is

especially important when organization extends across multiple generations of cells or organisms.

The analysis also emphasizes the constitutive importance of *Context*. Biological organizations persist through selective relations with environments that supply resources, impose constraints, and change through time. Ecological Coupling is not an external addition to an otherwise self-contained individual. At the same time, ecological dependence does not determine organizational membership. Maintaining this distinction allows biological organization to be analyzed as environmentally embedded without dissolving the difference between an organization and the wider ecological systems in which it participates.

Evolutionary explanation and organizational explanation address related but non-identical questions. Evolutionary theory investigates processes through which heritable variation and differential reproduction change biological populations and lineages. Organizational analysis investigates how particular biological organizations are constituted and maintain identifiable continuity through ongoing material, developmental, and ecological change.
Neither level of explanation replaces the other, and their relation becomes especially important where selection, reproduction, and organization occur at different biological levels.

The PSE contribution is best evaluated by whether its domain-independent concepts add explanatory value to these established biological distinctions. Persistent Organization may provide a common ontological vocabulary for analyzing continuity across materially different systems, while the six biological dimensions specify processes that cannot be derived from that ontology alone.
The framework becomes scientifically useful only insofar as it clarifies relations that would otherwise remain obscure, supports informative comparisons, or generates hypotheses capable of independent investigation.

This also defines an important limit. Recasting established biological phenomena in PSE terminology would not by itself constitute a theoretical advance. The value of the framework depends upon whether the proposed relations among Context, organizational differentiation, constraint, persistence, and identity improve explanation or empirical inquiry beyond conceptual re-description.
The comparative programme developed here should therefore be judged against established biological theories and against alternative accounts of biological individuality.

## 10.6 Concluding Reflections

The analysis developed in this monograph began with a problem that has become increasingly prominent in contemporary biology: the biological individual is difficult to identify through any single material, physiological, developmental, ecological, or evolutionary criterion. Cells, biofilms, holobionts, and eusocial insect colonies reveal different ways in which biological organization can persist while boundaries, components, interactions, developmental histories, and evolutionary relations change.

The comparison suggests that these differences are best examined through the organization of biological continuity. Organizational Boundaries, Organizational Integration, Adaptive

Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity identify distinct aspects of that continuity.
Their comparative value lies in showing how biological organization can be distributed differently across components, processes, environments, timescales, and levels of organization.

*Persistent Organization* provides the broader ontological concept through which such continuity can be analyzed within PSE. It accounts for the possibility that an organization remains identifiable through material and relational change. Biological Individuality requires further specification. The existence of Persistent Organization, even where several biological dimensions are strongly developed, does not by itself determine that a biological individual exists at the same organizational level.

This distinction is especially important for collective biological systems. Biofilms, holobionts, and eusocial colonies demonstrate that organization can extend beyond paradigmatic organismal boundaries without making collective individuality an automatic consequence.
The relevant question becomes how the different forms of biological continuity are organized, whether they converge at the level under consideration, and what biological evidence warrants treating that organization as an individual.

The same caution applies to *Organizational Scale Invariance*. The case studies identify candidate correspondences among organizational relations realized through very different biological mechanisms. They provide a basis for investigating whether comparable organizational architectures recur across scales, while leaving that proposition open to independent comparative and empirical testing.

The resulting account is deliberately incomplete. It does not supply a universal criterion of Biological Individuality, nor does it establish that the six analytical dimensions form a necessary and sufficient set. It provides a relational framework for comparing biological organizations and for identifying where different forms of continuity converge, diverge, or occur at different organizational levels.

The broader PSE proposition remains correspondingly open to criticism and investigation. Its scientific value will depend upon whether the concepts developed here clarify biological problems beyond existing terminology, support comparisons that established approaches do not readily provide, and generate consequences that can be examined independently.
Biological individuality offers a demanding test because biology repeatedly confronts systems whose material composition changes while their organization persists, and systems in which organization extends across entities that remain organized individuals themselves.

Biological individuality therefore cannot be reduced to material sameness or inferred automatically from organizational persistence. It becomes a question about the relations through which a living organization remains distinguishable, integrated, viable, developmentally continuous, ecologically coupled, and evolutionarily connected through time.

Determining when that organization warrants the attribution of individuality remains a task for biological theory and empirical investigation.

## Epilogue

The biological individual once seemed easy to recognize. A cell has a membrane. An animal has a body. An organism begins, persists, and eventually dies. Yet the closer biology has looked, the less secure these boundaries have become. Symbiosis, microbial communities, colonial life, and multilevel selection have revealed forms of living organization that do not fit comfortably within the classical image of the organism as a self-contained individual.

The difficulty may lie partly in the question itself. If biological individuality is sought as a property possessed by a particular kind of biological entity, every exceptional case appears to demand another criterion. If individuality is approached through organization, a different picture emerges.

The cases examined in this monograph occupy very different biological scales. A living cell, a biofilm, a holobiont, and a eusocial insect colony differ profoundly in material composition, spatial organization, mechanisms of coordination, reproduction, and evolutionary history. Yet each can sustain relations that distinguish an organization from its Context, integrate its components, regulate interactions, maintain continuity through change, and contribute to persistence over time. None of these dimensions alone determines individuality. Their organization together provides the relational configuration through which the attribution of individuality can be investigated.

Biological individuality can therefore be approached through the relational organization of living systems. Its boundaries may be sharp or diffuse, its integration strong or weak, its components stable or replaceable, and its continuity realized through different mechanisms. What persists is not necessarily a fixed collection of matter. It is an organization capable of maintaining a distinguishable trajectory through changing relations with its Context.

This perspective also changes the significance of biological scale. The comparison developed here suggests that similar organizational relations may recur in systems whose material realizations differ radically. Cells, microbial collectives, symbiotic associations, and insect societies need not be instances of the same biological mechanism for their organization to display comparable relational architecture. This possibility is formulated within the PSE Research Programme as Organizational Scale Invariance. It remains a research hypothesis whose scope and limits must be established through further comparative and empirical work.

The result is therefore not a new universal criterion for deciding once and for all what counts as a biological individual. It is a framework for asking a more precise question:

> *under which organizational and contextual conditions does the attribution of biological individuality become warranted?*

That question leaves the boundary of the individual open to investigation. It also places biological individuality within a larger problem. Living systems persist because organization is continually maintained under conditions that could have been otherwise. Components change, environments change, relations change. Identity survives only insofar as organization can survive those changes.

Biological individuality, on this view, is one expression of that deeper organizational problem. Life does not merely occupy a world already divided into individuals. Through organization, living systems continually establish, maintain, and transform the distinctions by which individuals become possible.

# Monograph-Specific Glossary

## Note to the Reader

The canonical terminology of the PSE Research Programme is defined in Monograph No. 1A — Canonical Glossary and Conceptual Dependency Map. The present glossary contains concepts introduced, substantially extended, or employed in a specialized biological sense in this volume. Foundational PSE concepts retain the canonical definitions established in Monograph No. 1A unless explicitly indicated otherwise.

## Adaptive Persistence

Definition

The capacity of a biological organization to maintain or restore viable organizational continuity under changing internal or external conditions through regulated change.

Adaptive Persistence concerns organizational responses occurring during the persistence of a biological system. It should be distinguished from evolutionary adaptation, which concerns heritable change across generations.

Cross-reference

See also:

* Persistent Organization (Monograph No. 1A)
* Organizational Integration
* Ecological Coupling
* Evolutionary Continuity

## Biological Individuality

Definition

The attribution of individuality to a living organization whose biological continuity can be analyzed through the relations among Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity.

In this monograph, Biological Individuality is treated as a comparative biological problem rather than as an automatic consequence of Persistent Organization. The six dimensions provide an analytical framework; they are not proposed as necessary and sufficient criteria for individuality.

Cross-reference

See also:

* Persistent Organization (Monograph No. 1A)
* Organizational Boundaries
* Organizational Integration
* Adaptive Persistence
* Developmental Continuity
* Ecological Coupling
* Evolutionary Continuity

## Developmental Continuity

Definition

Continuity among successive organizational states during the biological development or history of an organization.

Developmental Continuity is distinguished from persistence of an unchanged state, from reproduction that generates successor organizations, and from Evolutionary Continuity across generations.

Cross-reference

See also:

* Persistent Organization (Monograph No. 1A)
* Adaptive Persistence
* Evolutionary Continuity

## Evolutionary Continuity

Definition

Continuity across generations involving reproduction, heredity, differential reproductive success, and evolutionary change.

Evolutionary Continuity is analytically distinguished from the persistence of a particular biological organization and from Developmental Continuity within that organization. In collective systems, evolutionary continuity may occur at a different organizational level from physiological or developmental integration.

Cross-reference

See also:

* Developmental Continuity
* Biological Individuality
* Persistent Organization (Monograph No. 1A)

## Ecological Coupling

Definition

The continuing relations through which a biological organization interacts with and depends upon its biotic and abiotic surroundings.

Ecological Coupling does not by itself determine organizational membership. Relations may be necessary for persistence while remaining relations between an organization and its ecological Context.

Cross-reference

See also:

* Context (Monograph No. 1A)
* Organizational Boundaries
* Adaptive Persistence

## Organizational Boundaries

Definition

The biological processes and relations through which an organization remains distinguishable from its surroundings and regulates interactions relevant to its continuation.

Organizational Boundaries need not coincide with a single physical enclosure. Their biological realization differs among cells, biofilms, holobionts, and eusocial colonies.

Cross-reference

See also:

* Boundary (Monograph No. 1A)
* Organizational Integration
* Ecological Coupling

## Organizational Configuration

Definition

The particular arrangement and relations among the biological organizational dimensions examined in this monograph.

Organizational Configuration provides a comparative description of how Organizational Boundaries, Organizational Integration, Adaptive Persistence, Developmental Continuity, Ecological Coupling, and Evolutionary Continuity are configured and related within a biological system. It does not constitute an independent criterion of Biological Individuality.

Cross-reference

See also:

* Biological Individuality
* Organizational Scale Invariance

## Organizational Integration

Definition

The coordination and interdependence of biological processes or components contributing to the continuation of an organization.

Organizational Integration may occur within a single organism or across multiple biological entities. It is analytically distinct from Coherence, which retains its canonical PSE meaning.

Cross-reference

See also:

* Coherence (Monograph No. 1A)
* Adaptive Persistence
* Biological Individuality

### Organizational Scale Invariance

Definition

The PSE research hypothesis that comparable organizational relations may recur across differences in substrate, scale, and domain-specific mechanism.

In this monograph, cells, biofilms, holobionts, and eusocial colonies provide biological comparison cases for investigating possible cross-scale recurrence. The comparison identifies candidate correspondences; it does not establish Organizational Scale Invariance as a general property of living systems.

Organizational Scale Invariance does not imply identical structures or mechanisms across scales.

Cross-reference

See also:

* Organizational Scale Invariance (Monograph No. 1A)
* Domain-Specific Mechanism (Monograph No. 2)
* Organizational Configuration

## Supplementary Material

Supplementary materials accompanying this monograph are published separately and form part of the supporting documentation of the PSE Research Programme.

S0 — Reading Guide
S1 — Comparative Matrix of Organizational Dimensions
S2 — Conceptual Dependency and Programme Position
S3 — Annotated Core Bibliography
S4 — Extended Abstract
S5 — Figures

The supplementary materials provide reading guidance, comparative and conceptual documentation, an annotated bibliography, an extended synopsis, and publication-quality figures. They do not form part of the main argument of the monograph and may be updated independently where appropriate.

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