Relational Theory and Ecological Niche Modelling

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ABSTRACT

Relational theory is an extension of Robert Rosen's relational complexity. Its development implies a fundamental, four-quadrant 'holon' structure in nature based on nested modeling relations and their structure-function epistemology. Holons comprise and are comprised of other holons, thus providing a robust holistic analysis of nature at all scales. The four quadrants of the holon correspond with Rosen's theory, Aristotle's four causes, Ken Wilbur's analysis of social hierarchies, and Vedic principles employed in quantum physics. Two quadrants of the holon define mechanistic science while the other two account for complexity. To use this view of nature as an analytical method and informatics architecture, each quadrant must have its own methods and tools. The mechanistic components are well developed but the relationistic ones are not. Quadrant II represents intrinsic potentials in nature, and it corresponds with the concept of the ecological niche in Ecology. The ecological niche is thus indicated as having central importance in ecology and relational theory. We are in a good position for rapid development of Quadrant II, which requires a robust and general method for ecological niche modeling. Such a method is being developed and is described here as the General Ecological Niche (GEN) model. Once this general method is established in Quadrant II, development of Quadrant III methodology for interactions of niche potentials and their aggregation into system attractors, may also be accomplished. Coupling models in all four quadrants of the relational holon will provide an entirely new form of analysis and informatics that is appropriate for studying complex and living phenomena. Urgent development of this architecture is recommended to address ecosystem problems.

Keywords: Relational Theory, Niche Modeling, Theoretical Ecology, Complexity

INTRODUCTION

Relational modeling and informatics is a new field of research and development that is emerging from Dr. Robert Rosen's work on relational complexity (Rosen 1991). The author has been developing this theory as a general method for analyzing complex natural systems (Kineman 2007a). Recent developments suggest that a very special kind of

relational entailment – a 'holon' structure – exists throughout nature. Furthermore, the holon structure can be seen as both epistemological and ontological. In other words, when nature is viewed though relational theory both its explanation and its presumed 'reality' can be brought into harmony. This property is untrue of mechanistic theory and analysis, in which we adopt conceptual terms of reference that are 'ideals,' which abstract simple properties for investigation. For example, post-modern science has discovered that the concept of particulate objects does not apply to foundational 'building blocks' of nature. In contrast, the terms of reference to nature that comprise relational theory apply rigorously at all scales, making it a truly general theory of nature.

The 'relational holon' has a four-part structure. Holism can thus be defined in terms of that structure, and mechanistic analysis, which divides the whole into observer and observed, can be easily identified with one half of it. The other half involves, as best we can say, 'non-localized'[1] or contextual causes corresponding to Aristotle's formal and final cause. The four-quadrant holon structure corresponds with Robert Rosen's "modeling relation" as further interpreted by (Kineman 2008), and Ken Wilbur's four quadrant clustering of natural hierarchies evident from an extensive analysis of cultural reality beliefs (Wilbur 2007). The relational holon corresponds with ancient Vedic references to a fundamental relationship between "existence" and "non-existence" (as traditionally translated from the Sanskrit), that has four facets (the 'four faces of Brahman'). These same references were interpreted by the early quantum physicists (many of whom were Vedic scholars in their own right) as a fundamental relationship between "local" and "non-local" existence. That understanding is what led to the discovery, description, and practical application of matter-energy conversion. A number of them also realized, and wrote extensively, that this basic principle has fundamental importance in explaining life (Schrödinger 1943).
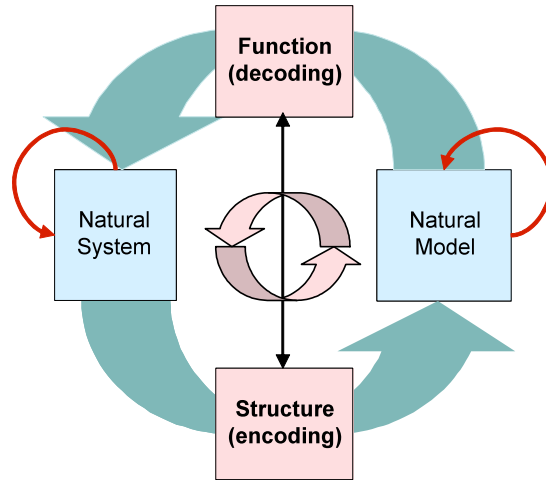

Figure 1: The Relational 'holon'
(based on Rosen's 'modeling relation')

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[1] Avoiding for the moment, but not excluding, the more technical meaning of 'non-local' in quantum theory.

Still, in the course of post-modern science, we failed to apply this fundamental relationship broadly. Its implications appear strange, even bizarre, to anyone cultured by the senses; which see, hear, touch, taste, and feel apparently fixed objects. The idea that those objects are appearances seemed unnecessarily abstract in most disciplines, especially at classical scales of investigation. So, we studied living organisms as objects, with important external properties and the presumption that internal properties are reducible to externals. Even in studies of humans, driven by an obvious psyche, the object-illusion has been maintained in theory and practice. This blindness has left a serious hole in science, and today it weakens our understanding of living nature in general to the point that urgent 'ecological forecasting' and 'ecosystem management' are little more than slogans because we have not developed adequate theory and methods to deal with ecological complexity. The need to do so is now critical as a result of misunderstood and ignored relational entailments between humans and the global system.

FOUR-QUADRANT ORGANIZATION OF THE HOLON

The 'relational whole' or 'holon' (from the Greek 'holos', meaning 'whole'; first coined by Arthur Koestler in 1967 to refer to something that is both whole and part) has four distinct analytical components that also lend themselves to holistic analysis. These are presented in **Figure 2**, oriented to Rosen's conventional presentation of his modeling relation (which is a mirror image of Wilbur's four quadrant cultural holon), with the localized system of interest on the left and its contextual representation on the right, as in **Figure 1**. We can easily see the two-part structure of mechanistic science on the left side comprised of quadrants I and IV (measured state and dynamics). Theory, methods, and tools for these quadrants are well-developed, and need only to be coupled with analysis represented on the right side of the diagram, quadrants II and III. The arrows in the diagram's outer ring, going counter-clockwise, indicate a deductive loop in which each quadrant is constructed on elements of the former. However 'construction' (in the sense of 'constructivism') is not mere assembly from the bottom-up; it also involves information from the top-down. Thus, an opposite inductive loop, with arrows going clockwise, is also involved. In this way, each quadrant itself forms a component holon, which is a special kind of modeling relation; one that translates between epistemological and ontological elements. It is the nature of holons that they comprise, and are comprised of, only holons; hence the analysis is 'holistic.' This may seem like a difficult principle to apply generally, but a simple example will demonstrate the principle. In Rosen's extensive treatment of 'measurement' (Rosen 1978) it becomes clear that simple abstraction is the goal (*"nothing is more abstract than a number"*) and yet complex relations are involved. Every natural interaction is, in essence, a measurement. And every natural interaction must also be an interaction of whole systems, which are complex. Hence measurement is a special kind of holon that abstracts simple empirical properties from complex ontological wholes.

Quadrant III appears to be the most mysterious to modern science (but the most obvious to spiritual practitioners), corresponding to Aristotle's 'final' causation. In the counter-clockwise deductive cycle, quadrant III obtains from an aggregation of the elements in Quadrant II (the elements that go into the contextual image or implicit systemic 'model').

However, quadrant III, like all the other quadrants, cannot be reduced to its component parts because formative influences also arrive in the reverse direction, through the inductive loop. That is what gives rise to seemingly mysterious emergent properties, such as intentionality, that translate potential (quadrant II) into system attraction and anticipation. Anticipation thus results from 'knowledge' of the subsequent holon; i.e., how the model will be expressed and where. For this reason the outer ring arrows in both directions should be thought of as information relations, in the sense of formative inductions.
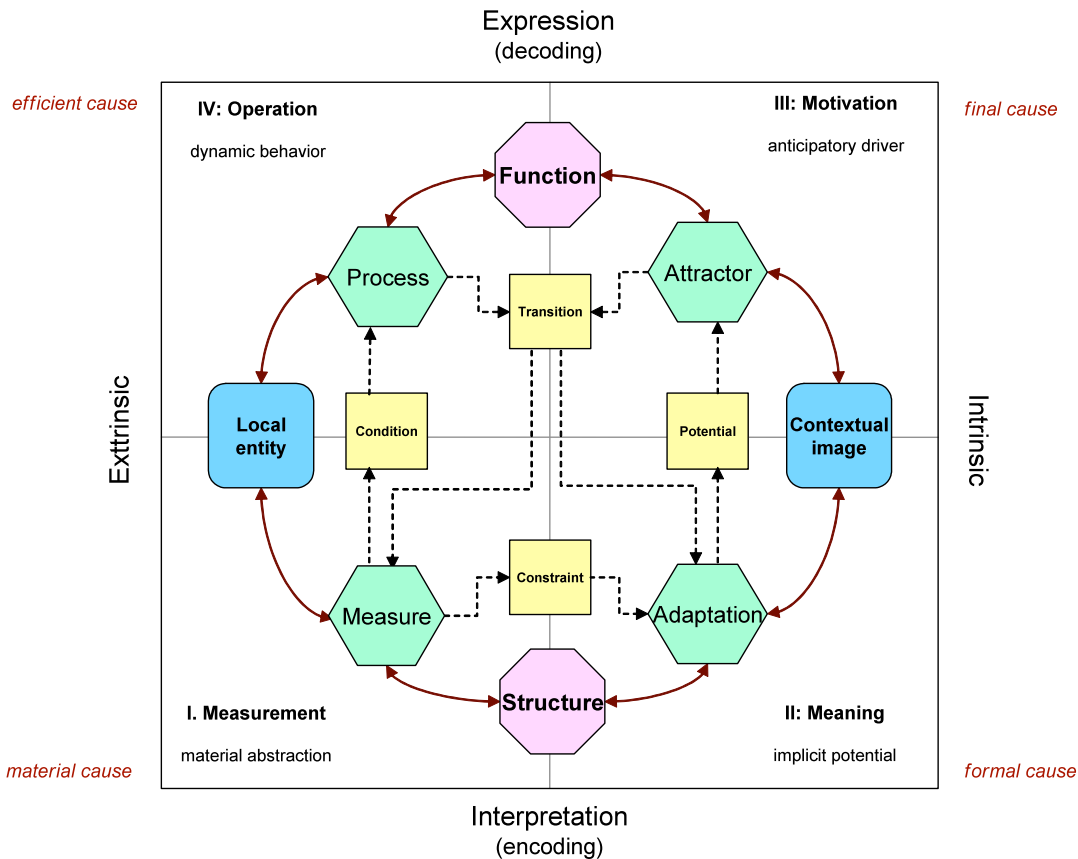

Figure 2: Four-Quadrant Structure of the holon

To further grasp that none of these quadrants are mysterious, notice that the aggregation of elements in quadrant II (as system potentials) along with emergence of a new animating property appearing in quadrant III (attractors), is entirely analogous to what we find on the mechanistic side, where 'dynamics' can be decomposed into the aggregation of states (from quadrant I) with the addition of supervening 'forces' that animate, i.e., alter the states.[2] Hence, while mechanism can be said to be 'state-based', 'relationism' (a term I propose, to parallel and contrast with mechanism), can be said to be 'potential-based.'

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[2] In the early days of Newtonian Mechanics, many critics considered the idea of 'force' to be highly mysterious. Hertz, for example, considered it entirely mystical 'action at a distance' and preferred the model of a continuous material ether to account for motion. Hence he founded wave theory.

Where in science do we have the theory, methods, and tools to work with 'potential-based' systems? The practical approaches that exist are scattered and disorganized because we do not have a central theory to gather them into a coherent framework. Furthermore, where tools exist, they tend to be developed for limited applications, their general applicability (as indicated in the holon) being unapparent to most people. Worst of all, a convention has developed, mostly carried over from positivistic science, to treat the intrinsic domain as illegitimate. Methods and tools for exploring the domain of system potentials, while a practical necessity in many fields, are often treated as heuristic and instrumental approaches that must ultimately be subjected to the rigor of mechanistic theory alone. That attitude declares the theoretical generality of systemic potentials (quadrant II) and their informed, attractive aggregation (quadrant III), which allow a system to be complex, anticipatory, and even intentional[3], to be non-existent from the start, and not worthy of investigation. I wish to shatter that view once and for all by declaring what now seems obvious: Only entire four-quadrant holons are real and natural. What we observe of nature is a fragmentation of that reality, and we are generally trying to understand nature through these fragments.

Ecology and many other fields need a way to understand and work with complexity in nature. Living systems are characterized by complexity but we do not have a generally accepted theory of what complexity is, let alone how to represent it in science. There are many computational theories of complexity, but few that reach to the origin of the phenomenon itself. The relational theory and holon organization referred to here can provide the needed theoretical framework that is open enough to explore many new kinds of phenomena, while retaining the ability to describe systems that exhibit less than the full set of properties in all quadrants. There is nothing in this analysis, therefore, that alters our knowledge of mechanistic systems except at their most fundamental level, where we already know complexity exists. The picture of nature that emerges is one where complexity in terms of holon relations is the fundamental reality from which both mechanical and living systems emerge; the first being a reduction of the holon (to Quadrants I and IV), the later being a special arrangement of holons (described in (Kineman 2008)).

ECOLOGY AND THE SECOND QUADRANT

If we are to discuss 'potential-based' systems (the right side of the relational holon diagram), or to discuss whole natural systems, which require coupling potential-based and state-based systems, it is essential to generalize the concept of potential and to establish a methodology for modeling it.[4] I believe the need for this is no more obvious anywhere than

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[3] As opposed to particulate potentials that are localized and purely reactive.

[4] I do not claim to be introducing this idea for the first time. There are many approaches in the 'softer' sciences that describe system potentials and their effect. In physics itself, thermodynamics and aspects of quantum theory come closest to being system 'potential-based' descriptions. Information theory has also crossed a threshold where context and potential must be considered, as in the development of semantic webs and networks. It is not surprising, therefore, that when one needs to describe a complex system of formal and final causes, it is done in terms of some combination of thermodynamics, quantum theory, and information theory. In these cases, however, an ethic is often preserved that the stranger system properties must be

in ecology. Ecology is fundamentally a relational science, but not in a trivial sense of 'things' relating to 'things.' It is about the relationship between organisms and their environments, which is a formative tension bridging potential and actual conditions through adaptation, and bridging past and future conditions through evolution. Environmental or ecosystem context acts systemically, in a diffuse, non-localized way owing to the anticipatory nature of the organism.

Because of its fundamental reliance on the relationship between organism patterns and their environmental or ecosystem contexts, Ecology is first and foremost a '2nd Quadrant' holistic science. Aspects of "Deep Ecology" (Sessions 1995) and "Vedic Ecology" (Prime 2002) reach into the 3rd Quadrant, which is why aspects of ecology can have a spiritual character. It is not a perversion of scientific rigor, nor an addition of personal subjectivities; but the genuine presence of Quadrant III. To understand how one quadrant is constructed on another and tied to the most fundamental organization of nature is certainly one place ecology should be allowed to go. However, we must go there in explicit, practical steps. Science is about linking significant detail with general theory, and while a general theory of the relational organization of nature in terms of four-quadrant holons may be the needed framework, each quadrant must be meticulously developed with practical methods and tools of its own. In that regard, it is reasonable to ask if the attention begin given to each quadrant is in proper proportion.

Considering the four quadrants, we might guess that science has placed and continues to place an overwhelming emphasis on two: Quadrants I and IV. It seems to place tentative effort in Quadrant II in terms of niche theory and adaptation, and speculative attention to Quadrant III in terms of complex potential. And yet it is probably not the case – nothing in this analysis can suggest so – that 'most' of nature exists on any one of these quadrants. All of nature is a balance of all four, while each quadrant is appropriate for addressing different kinds of questions. The issue then becomes, "are we asking the right questions" with regard to the complex ecological changes that are present and on the immediate horizon?

We are currently in a good position to address the rigors of Quadrant II. The essence of Quadrant II turns out to be none other than the ecological 'niche' concept. The ecological niche is indeed open to modeling but so far this has not been done in a theoretically general way. Nevertheless, niche models have been extensively applied to a variety of questions regarding past, present and future distributions of organisms (Peterson 2003; Peterson 2006; Roura-Pascual et al. 2006). They have also been used to show areas where

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thought to correspond at some limit to the presumed "underlying" dynamics of a mechanism. The very limited scope of that assumption can be seen, for example, in information theory, which is still largely based on "transmission" models, where something called 'information' moves as if it were a physical object, ignoring the influence of the receiver on the transmitter, reducing the role of context to noise, and purposely separating information structure from semantic interpretation (meaning). These were, of course, the goals of World War II cryptography research, which had a very narrow interest in ways to structure 'information' so as to *prevent* general understanding. The early information theorists working in cryptography research (which included the founders of information theory, Shannon, Weaver, and Werner), were studying how to separate semantics from syntax for security purposes; whereas holistic science today, and certainly ecology, needs to understand how syntax and semantics are naturally connected.

populations of species are likely to occur, helping to target sampling efforts and providing a more robust assessment of biodiversity (Guisan and Zimmermann 2000). Niche models have been used for many other purposes, including protected area design, invasive species prediction, epidemiology (disease vectoring), and more. There was even an attempt to use niche models to catalog the niches of all known species (the "LifeMapper" Project).

The niche concept has had a varied history of interpretations and the current approaches are very narrow in their scope and design. Most niche models today are statistical correlation techniques aimed at "predicting" geographic distributions from samples of the distribution. The idea of prediction and hypothesis testing is taken in a purely statistical sense, to mean how well the output pattern matches reality as observed (presumably using different data). A review of how niche models in use today (including GARP, Maxent, Linear Additive, Multiplicative, and others) compare and how accurate they are revealed that they do not match reality very well at all (average correlations of Pearson's $r = .2$), and that they differ among themselves by as much or more than their accuracy, with each model doing better under different conditions (Elith et al. 2006). Furthermore, being mere statistical or genetic correlation techniques, they provide no support for experimentation to explore the ecological reasons for their differences or errors. They are matching exercises with little or no scientific analysis capability (with a few exceptions). We can see that many if not most prior applications of niche modeling, while representing steps forward at the time, have embodied a serious design flaw in that they attempt too much in one step.

It is thus entirely understandable why correlative niche models do a poor job of predicting a living distribution pattern (and why statistical analysis is a component of, not a substitute for, basic science). The reason is clear in the holon structure discussed above. The niche model establishes a system potential (Quadrant II) that may or may not be realized through the complexities of Quadrants III and IV. Not only are other niche potentials (from interactions and associations coming together in Quadrant III) involved in the realization process (Rosen's 'decoding'), there are also subsequent (and pre-conditioning) dynamics involved in Quadrant IV. It is necessary to couple three very different kinds of models, with feedbacks, to take a niche potential all the way from an interpreted pattern to a forecast of actual conditions over time (even the present time owing to the effects of historical dynamics and system memory). This does not mean that simple correlative techniques to estimate distribution potential have no use; but that their use must be more carefully understood. In particular, many current built-in techniques for model 'validation' show only model fidelity to the input data, and have nothing to do with validating prediction of the larger distribution.[5]

Some intriguing attempts have been made to couple ecological adaptations with dynamics, treating quadrant III simply as a domain of interaction. For example, "agent based modeling" (Langton 1995) linked behavioral rules with dynamics for multiple interacting free agents ("The Game of Life"). While certainly better than static estimation, it would likely be improved by more explicit representation of each quadrant. Non-linear behavior represented in ecosystem 'flips' (from one stable organization to another) have been studied from the perspective of chaos theories (Kay 1997), with definite implications for

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[5] Because the statistical inference assumptions do not hold as a consequence of complexity.

systemic potentials and "attractors"; but still not an analytic way of working directly with those potentials. Hierarchy theory (Allen and Starr 1982) follows very closely Rosen's relational concepts of the whole, as does Ascendency theory (Ulanowicz 1997); and these may represent some of the best theoretical entries to Quadrant II and III so far. Network analysis (Chen and Ware 1999) certainly has a role to play, as did Emergy analysis (Odum 1996), and Adaptive Management (Holling 1978). The field of ecosystem dynamics has heavily emphasized the discovery of mechanisms; important in their own right but missing more subtle (but often more significant) phenomena that may be accessible through relational analysis. We have generally persisted too long in the idea that organisms only react to their environments, whereas it is clear that influences go in both directions (Odling-Smee, Laland, and Feldman 2003; Lovelock and Margulis 1974), and in complex entailments.

There have also been many attempts to use process modeling alone (Quadrant IV) to predict distributions, and generally this effort has done more poorly than statistical techniques (one reason the statistical methods have flourished). The presumption in such efforts is that system complexity will be reducible to processes, if they are considered in enough detail – the mechanistic paradigm. But they are not. Each quadrant must be modeled in its own right and then coupled, because each represents a different class of phenomena, in Aristotle's terms, a different kind of causal explanation.

EARLY APPROACHES TO ECOLOGICAL NICHE MODELING

The ecological niche concept was introduced by Grinnell (Grinnell 1917) and Elton (Elton 1927), and later became defined by Hutchinson's "n-dimensional niche" concept (Hutchinson 1953), and McArthur's quantification of "resource axes" (MacArthur 1972). As adopted in ecology, the niche describes the constraint relationship between an organism and its environment (Odum 1953). Liebold points out that in practice the niche concept has also been used to describe "impact" on the environment in addition to Hutchinson's concept that focused more on resource "requirements" (Liebold 1995). This difference shows up in the distinction between habitat requirements and organism function (function performed). These ideas combine in the concept of "niche construction" (Odling-Smee 1988) where the effect of *'what an organism does'* (Rosen's definition of its function, when context is considered) can be considered in assessing *'what it requires'* (the ecosystem functions or 'services' it receives). Niche theory has also been used in social science, notably to assess *"how differential ecological strategies attract participants"* (Eighmy and Jacobsen 1980). The three traditional interpretations of the niche are combined in relational theory: (1) as a constraint on the distribution of functional units according to their adaptive requirements, (2) as a constraint on the expression of functions, and (3) as an attractive or even anticipatory potential for niche occupation. Since the niche describes the suitability of a function, and functions change states, the niche is active, selecting potential changes while attracting agents.

Early approaches to niche modeling in the US Fish and Wildlife Service centered on the development of "Habitat Suitability Indices" (HSIs). HSIs, however, were *"not research*

models" but *"practical, operational planning models designed to assess impacts of change"* and *"a bridge between the fields of planning and science"* (Schamberger and O'Neil 1986). Chalk, however, reported poor prediction results from HSIs due to unconsidered dynamics and scale issues (Chalk 1986). Subsequent reviews (Scott et al. 2002) indicated dramatic improvements in the preceding two decades, although with considerably more work needed, particularly on issues of scale and dynamics (O'Connor 2002).

Habitat Suitability Models (HSMs) were a more quantitative approach succeeding HSI's. They were early niche models that were successfully applied where equilibrium assumptions held (Nielson 1991; Rubec et al. 1999). Today's ecological niche models can be considered further developments along these lines, taking advantage of Geographic Information Systems (GIS), which have become a primary tool in mapping habitat and species distributions. These developments also brought the recognition that GIS and other spatial analysis tools must be effectively integrated or linked with various kinds of models (Goodchild, Parks, and Steyaert 1993; Goodchild, Steyaert, and Parks 1996). Nevertheless, a general method for doing so has not been established.

The term 'habitat' is generally taken to mean the place where a population of related organisms live. This concept breaks down when discussing whether or not the habitat is occupied, or in discussions of what might be suitable habitat for relocating a population. That definitional problem was partly overcome by the ecological niche concept, but similar differences have arisen there too. The term 'ecological niche' most commonly means *the suitable conditions for occupation by a given population of interrelated organisms*. Whereas habitats exist in geographic space, niches exist in environmental space. The two relate in terms of how environmental factors are distributed geographically and how niche potentials are occupied (i.e., 'realized'). It is thus possible to speak, as is commonly done, of the 'potential niche' (more properly 'niche potential') and the 'realized niche' from which we infer habitats in real space and time. The reason for confusion in these definitions is relational complexity. The definitions necessarily involve both potential-based and state-based systems acting together, and it is very easy to get into circular definition problems.

The primacy of the organismic niche concept has been emphasized by many authors (Scott et al. 2002). Concerns regarding dynamics, heterogeneity, and scale (Wiens 2002), have been addressed by:
  (a) Introducing innovative 'control variables', such as a niche variable defined on metapopulation matrix requirements (Gehring and Swihart 2003; Stacey and Taper 1992),
  (b) Distinguishing niche components for corridor, source and sink habitats (Rosenberg, Noon, and Meslow 1997; Mabry and Barrett 2002), or
  (c) Iterative succession of models simulating dynamic changes in habitat controls.

It is now commonplace to infer distribution of organisms by correlating their known occurrences with variation in environmental parameters, and thus to produce some form of environmental signature that can be mapped as a potential distribution (an estimate of

suitability or probability of occurrence). Measures of ecological response along resource axes are usually quantified as gradients in environmental conditions, thus quantifying potential distributions (Austin 2002). This dimensional analysis is distinguished from generalized habitat classifications, which may not be specific to any given organism, and a wide range of other ecological mapping methods and philosophies, However, as Austin and Meyers understated: *"failure to recognize the various shapes of response curves may result in inefficient or incorrect predictive models"* (Heglund 2002).

Selection of appropriate controlling variables is essential, as is selection of a robust technique for combining dimensional response curves into an n-dimensional niche hypervolume. The semantics of model construction (ecological meaning) are of prime importance with regard to selection of techniques, as emphasized in two major reviews of distribution modeling (Scott et al. 2002; Verner, Morrison, and Ralph 1986). Hence, niche models should be transparent with respect to their assumptions and method of constructing and applying response functions; and they should allow for ecological, not just statistical hypothesis testing.

Problems in niche theory and modelling

Only a few niche models attempt to apply ecological theory as distinct from statistical theory. The body of probability and statistics theory has shown it to be robust, and thus scientifically defensible, but this does not mean it therefore represents the best or deepest analysis of a living system. Ecology requires its own inferential elements. Probability and statistics apply to everything that can be set against a background of random events, as a means of detecting and quantifying non-random events. But it does nothing to explain the source of non-random behavior or to detect adaptive distributions that conform to their backgrounds. These questions require experimentation.

Partly because of its over-emphasis on probability and statistics theory, niche modeling in general has not developed its potential for analyzing adaptation. It has primarily been a tool for interpolating observed patterns. The difference is significant because the ecological niche has to do with adaptive strategy, the result of which can be many different kinds of patterns, even ones that appear random. In ecology a random distribution may not have the same meaning that it does in a physical system. Ecological distributions that correspond with the distribution of factors may be highly dependent on those factors (or not), whereas a physical distribution that does so is presumed to be entirely independent (since adaptation cannot be involved). An emergent biological pattern that seems random, or stochastic, cannot be interpreted as a null effect. The principle of adaptation in ecology demands an explanation for a pattern, even if it appears random with respect to other distributions.

On the most fundamental level, theoretical ecology itself has always had problems (Simberloff 1981). Attempts to find a foundation for ecology in physical theory, which were hotly pursued in the 1960's, have generally failed. Relational theory exists prior to physical theory because it explicitly represents potential states and entails them with actual states. This is what makes it suitable for ecology. The niche can then be seen as the proper

scientific description of system potentials that govern possible futures. What are these potentials and in what way are they real? This question is at the heart of relational theory, which establishes potentials as implicit 'model' images, embedded systemically.

Confusion about the fundamental assumptions of ecology can be seen in Gaston and Chown's recent challenge to niche theory. Their concept of *"niche neutrality"* (Gaston and Chown 2005) was interpreted by many as challenging the fundamental niche concept itself. However, the term actually applied to a rather unique situation; a very stable and climatically uniform tropical forest where species distributions appeared to be stochastic rather than niche-segregated. The study showed that species occurrences were randomly distributed in a homogeneous environment. If one were to adopt traditional physical assumptions, that random distribution means no effect, the interpretation would be that there is no adaptation. However, that is an incorrect interpretation. In a region of fairly uniform suitability for multiple species, one might expect to have broad, flat, overlapping niches, within which spatial dynamics and interaction would dominate.

It is well known, for example from studies of Serengeti ungulates (Sinclair and Norton-Griffiths 1995), that when resources are productive and uniform, animals can co-exist (resolve the tension of overlapping niche potentials) by segregating resource use by time of day – a behavioral adaptation. Stochastic distributions in space cited in niche neutrality theory may be an analogous solution to the problems of a relatively uniform, shared niche. Stochastic or temporally segregated distributions can thus arise from niche overlap. Such factors cannot be combined directly as part of a niche potential because they exist in different domains (quadrants of the holon); however, both kinds of phenomena can be considered at different stages of the modeling and mapping process. Supposed niche neutrality, therefore, does not violate the assumptions of niche theory; it only demonstrates what is presented here; that niche theory is only part of the picture, the centerpiece of Quadrant II.

Another result of the tendency to replace ecological theory with statistics and probability theory has been an inappropriate mixing of niche factor variable types. The niche concept traditionally applies to how organisms (usually aggregated by species) are both *supported and limited* in some measure of their viability (abundance, biomass, density, etc.) within an ecosystem, but it has also been applied to represent how the presence of organisms is *indicated* by associated phenomena. Often these two types of analysis are conflated, producing ambiguous results. The difference is obvious between models that take the product of biotic response along resource axes, and those that take the sum. The former is an expression of adaptation to a set of factors, while the later is a compilation of evidence from factors, or probability of occurrence. These are very different phenomena, and a model should be of one type or the other, not mixed. As developed here, the ecological 'niche' refers to adaptation, which is expressed by ecological relations acting as a whole to limit suitability to optimal domains. Indicators of occurrence act independently and are not part a niche specification. Such 'proxy' models, however, can be very useful surrogates for a directly observed population distribution, either for input to a niche model or for use in validating a niche model. True niche factors, on the other hand, represent limits and optima along resource axes, which is the meaning of a functional response curve.

Geography is also a separate consideration entering in Quadrant IV. The environmental niche constitutes a potential, and as such it should be distinguished from geographic phenomena, which pertain properly to the 'realized niche.' Geographic proximity and associated dynamics that may lead to various distribution patterns are part of niche realization, not niche potential. Accordingly, niche theory should not be taken to pinpoint actual locations of adaptive entities (organisms, taxa, sub-functions, etc.). Instead it should be understood to be a study of adaptive potentials that are 'attractive' in the sense of drawing the organization of the system toward realizing those potentials by various means. This understanding of the situation then allows us to consider niche realization more broadly, to include not just occupation by the focal species but other ecological and evolutionary possibilities, such as functional replacements and evolutionary convergence. Due to environmental heterogeneity the translation of a niche specification into geography may produce patches and gradients of occupation, or relatively homogenous regions in which other dynamic or stochastic patterns emerge. Instead of being 'neutral' the niche potentials may be better understood as being in dynamic tension where adaptive resource partitioning cannot be accomplished by adaptation to physiological factors alone. Space and time interactions also matter, and in such cases it could be that behavioral adaptations may be expected to dominate.

Although it may be reasonable to say, as claimed here, that nature is entailed more like the holon than any other known organization, it is philosophically the case that nature is not like any analysis. We must consider it more seamless; whereas the components of analysis, even holon analysis, have to do with epistemological limits and how to come closest to overcoming them. We can only approximate what nature is really doing by coupling model types; that is, by relating niche hypervolumes with attractors and with spatial and temporal processes. But it is for this very reason that the ecological niche, if properly generalized, retains a central position in ecology, similar to that of evolution in biology. It is the means by which we can represent instantaneous feedbacks ("impredicativities" in mathematics) where inputs depend directly on outputs and non-localized effects of context. Only when taken together can the potential and realized niches be said to drive adaptation and evolution. Keeping this distinction between potentials and their realization is critical in relational theory and in the broader application of niche modeling.

Soberon and Peterson (Soberon and Peterson 2005) distinguished between mechanistic (dynamical) processes involved in distribution, and the relationship between sample and correlated factor distribution. They pointed out that while attempts to model the former (dynamical models) have difficulty when dealing with complex species interactions, attempts to model the later (niche models) tend to be confounded by their implicit inclusion of interactions and spatial dynamics, such as historical events, growth, dispersion, etc. Surprisingly, however, they propose to define the 'fundamental niche' in terms of bio-climate alone. Relational theory makes it clear that the fundamental niche must involve all external factors to which there may be adaptation; not just bio-climate. In that case, density, spacing, interaction, or other space-time factors in adaptation, must be considered part of the fundamental niche. The fundamental niche is thus ontological, whereas defining and relating potential and realized niches is the appropriate

epistemological method to represent the fundamental niche, which exists in all dimensions; dynamical, spatial, temporal, environmental, and even psychological.

THE GENERAL ECOLOGICAL NICHE (GEN) MODEL

The ecological niche can be defined generally such that it becomes the central concept of quadrant II. The general niche is a systemically established potential for viability (or 'suitability') of a given function. This definition certainly includes the traditional concept of the niche as representing the viability of a population of related organisms, but it may also be extended to represent the viability of sub-functions of such populations (e.g., the breeding or feeding niche), or super-functions (as in functional clusters adding up to ecosystem services), or, in fact, functions of anything. There is no reason why we cannot discuss the niche space of tourism, communism, impressionistic art, malaria, the 'old west', and on. Generalized thus, the niche concept can describe any system potential that establishes suitability for a function or set of functions. The general niche is about the systemic potential for functions, not structures because it is always a relationship between structure and function. 'Structure' and 'function' have been clearly defined in relational theory (Kineman 2007b; Rosen 1971). The environmental dimensions of the niche are structural (i.e., measurable). In fact, the inverse niche, i.e., the functionally determined viability of a given structure, is represented in dynamics (Quadrant IV). There, state transitions are explained in terms of natural functions, codified as laws of nature.[6]

In a recent project in India the author and a team of scientists compared dominant niche models across multiple case studies, examining their implicit assumptions of the models by de-constructing their outputs into functional response curves, and comparing them with the General Ecological Niche (GEN) model designed by the author. The preliminary results of that study show that each current model can be classified within a domain of all limiting functional response types (**Figure 3**). However, few if any of the current models are clear about what functional response type they assume, each claiming to be uniquely better for one reason or another. If niche modeling is to be generalized for broader scientific use than just species distribution modeling, and even for species distribution modeling, we must understand that there is no a-priori rationale for which response type in **Figure 3** is 'better' than another. The issue is one of experimental design, the presumed nature of the population being studied, and the question being asked. The GEN technique covers the entire domain, and is capable of modeling any of these types according to the ecologist's design. Once we exit pure statistical estimation and enter the arena of scientific experimentation, niche modeling becomes a tool for ecological inference and hypothesis testing about actual response to limiting factors.

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[6] This newer understanding may seem to reverse my previous opinion that it would be impossible to define an analytical function-space in which structural viability can be modeled, and that in any case, it would be redundant with the functional niche definition (Kineman 2007b). I did not see at that time, that dynamics is nothing but structural viability in a function space, quadrant IV; however it may still be the case that only dynamics based on general physical laws can be modeled directly; whereas modeling the effect of system-specific functions requires the entire holon structure.

We can infer a general ecological niche from any pattern that is functionally adapted to a given context. Factor selection and preparation of factor data is very important, however. Ecological factors are those to which the function being modeled has an adaptive relation. The factors should be defined in such a way as to expect a modal response. For example, "availability of water" may not be a good factor definition if the definition does not include the possibility of 'too much' water. The niche defines the suitability of a function that remains after mutually limiting factors have been combined. The mathematical model is a multi-dimensional functional response surface in n-dimensional factor space (where the factors are observables); generally referred to as a 'hypervolume.'
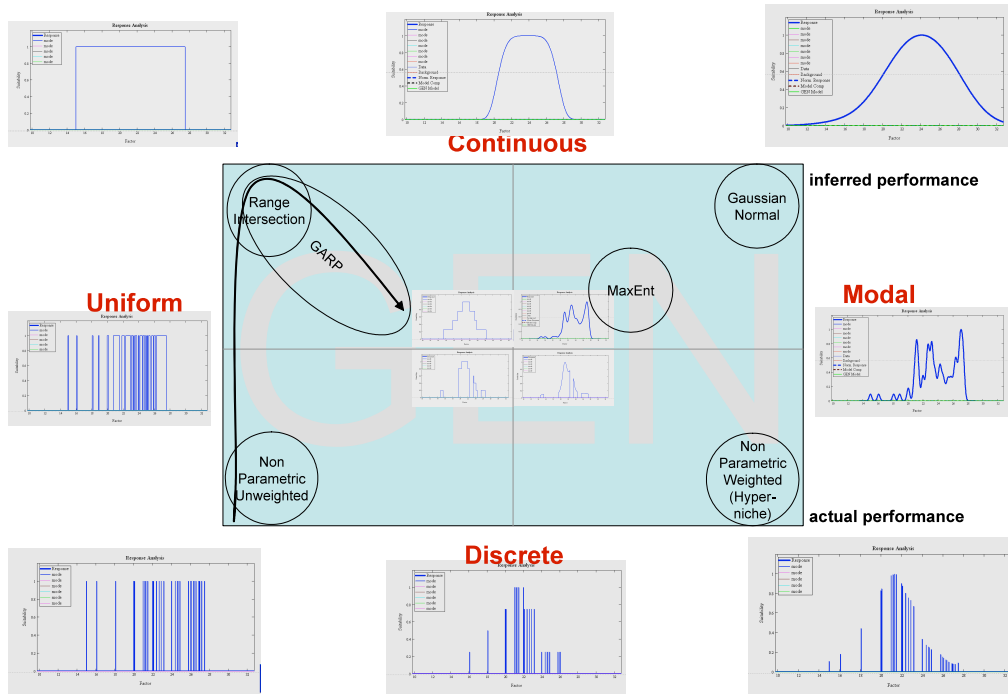
Figure 3: Domain of GEN and Functional Response Types

An example of response analysis in GEN from the India study (Rhacophorus malabaricus, a frog in the Western Ghats) demonstrates the difference between statistical assumptions and more ecological reasoning. **Figure 4** shows a typical response curve in one dimension (temperature) from the GEN factor analysis module. The solid blue curve is the density function of the original data with two peaks. The red curve is the background distribution in the vicinity of the samples. Both curves are normalized to a maximum of '1' (highest relative suitability). In this example, one might expect the right-hand peak in the data to be in part a result of background bias (since they coincide) unless the sampling design corrected for that (by stratification or other means). But removing the background bias from the data distribution is not a simple matter of taking the difference (i.e. difference from a random distribution, which would obviously follow the background). Even if the response function exactly matched the background, we could not conclude that it distributes independently of that factor, because it is adaptive; and yet sampling would almost certainly be biased by the background factor availability (again, if that bias were

not previously removed by the sampling design, which is rarely the case with biodiversity data).

Hence, expert judgment and scientific experimentation are requirements in interpreting response data, and no automated technique can claim to be best. In this example, the background correction was weighted to reduce the right-hand peak by about 50%, recognizing that there is very likely a significant bias in the data, but also recognizing that organisms were indeed observed at that factor value and may well be adapted to that value. It is also not easy to say, as in a 'signal to noise' sense, that peaks differing from the background distribution are necessarily more adaptive or optimal just because it differs from random. If the population is generally well-adapted to background conditions, as one might expect in a stable evolutionary environment, the left-hand peak may indicate competitive niche segregation, recent disturbance, or some other reason for skewing the distribution away from its optimum. There is clearly no single correct way to interpret the response function; the true value of such analysis lies in establishing and testing hypotheses to determine which case is true and which factors are important, and if there are other factors that may explain the distribution.

Once the modeler has determined what to model and why, it is then most useful to approximate the distribution with a parametric curve that generalizes according to the hypothetical distribution being tested. For example, one's hypothesis may be that the sample is from a single, commonly adapted species that should have a uni-modal response. One may construct that model for testing, or test a suspicious second peak. Only a parametric model can be manipulated in this way or extended theoretically beyond the data or interpolated between the data, which itself constitutes an hypothesis in ecological theory. **Figure 5** shows the GEN model (green), which is automatically generated from the corrected distribution (blue dashed curve), using a generalized Gaussian distribution (GGD) model. The model is generated asymmetrically to account for skewing (which may be ecological or physical, but nevertheless representing an unknown transformation of the axis.

As we saw in **Figure 3**, it would be entirely legitimate to model the distribution as discrete points, if, for example, one had sampled a highly diverse assemblage of organisms, or in an intermediate case, if one suspected or was testing for the presence of a sub-population with different adaptation; or if one simply wanted to map the most conservative distribution for initial testing, to reduce field costs. By including all these options at the scientist's discretion, GEN can support a range of ecological hypothesis testing. The same technique can also be used to decompose functions into sub-functions or to compose functions into functional clusters or ecosystem services. Multi-modal distributions can be modeled as such, or analyzed to determine the cause of multi-modality (sampling alias, existence of a sub-species, or sub-functions of a single species, etc.).
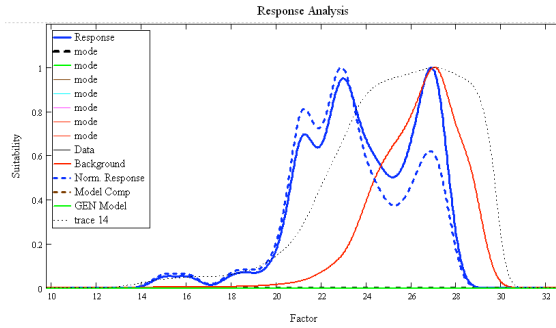
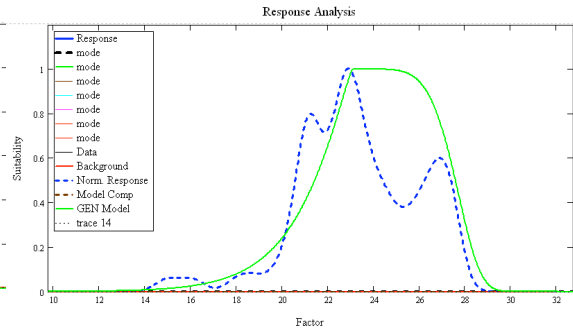Figure 4: Response Function and Background Bias Correction

Figure 5: GEN model (green) of the Bias Corrected Response (dashed blue)

Once the functional responses along each axis has been determined for experimental purposes, they are combined to form an n-dimensional niche hypervolume, as shown in **Figure 6**. **Figure 7** shows a typical output when the n-dimensional hypervolume is applied in geographic space. The colored distribution is the model projection; in this case a continuous distribution based on the occurrence point locations (white).
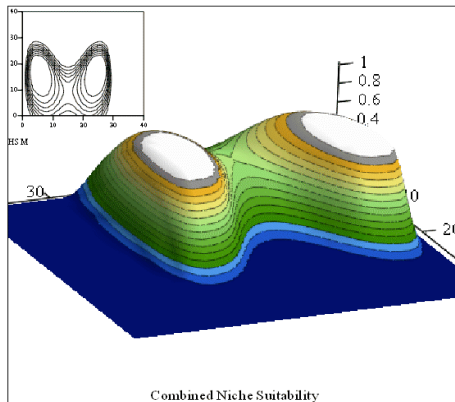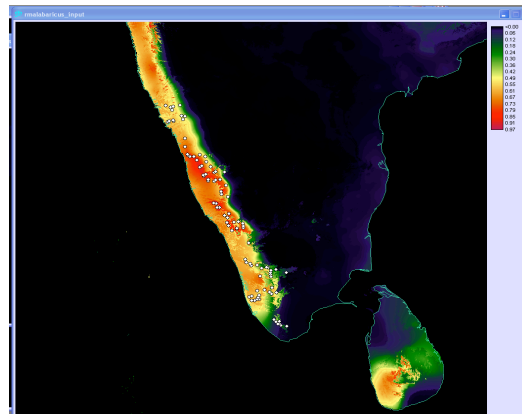

Figure 6: Niche

Figure 7: Niche Model Output Map

GEN is designed on relational principles and with the intention of occupying the central position in Quadrant II of the holon analysis, as discussed above. If the model is to be used as part of such a broader informatics architecture, parametric representation of the model itself is essential. Because such models represent potentials (after iterative testing), not actual distributions, their map outputs translated to geographic space, are temporary products intended best for experimentation, and they need not be saved except in model form. In a relational analysis, the niche model would be coupled with interactive models in Quadrant III and dynamic models in Quadrant IV.

When considered in the larger holon analysis, the niche represents a non-localized system regulation of functions – a kind of natural control information (Corning 2001). As niche potentials interact and form complex system potentials, they act to regulate processes. Coupling niche models with interactive and process models is relatively easy, but complex influences in each quadrant, and at each level of relational entailment, exist and may (for a

given study) need to be tracked and considered. In other words, complexity enters in each of the four quadrants due to other relations, such that coupling involves many possibilities. Adopting the holon organization for entailment of the informatics system itself thus mirrors the suspected entailment of nature and allows the means for capturing and working with complex linkages. This possibility constitutes a new kind of informatics in which proximal relations can be identified and entailed to allow one to construct complex queries, simulations, ecological forecasts, management scenarios, and to address many other questions about components or the whole system.

CONCLUSION

Relational theory extended to the theory of holons presented here, shows the distinction and need for coupling of four different kinds of scientific inquiry and analysis when considering complex or living systems. Each of the four quadrants of the relational holon is open to its own kind of modeling. Since complex phenomena involve all four quadrants, it is necessary to develop the modeling methods of each in its own right, but in a general way so that they can be coupled within a larger system of "relational informatics."

With few exceptions, niche models have been instrumental applications of arbitrary mathematical patterns with little if any claim to testing or applying ecological theory. Mere correlations without consideration of the theoretical reasons for them do not help us learn more about ecology. The construction of a General Ecological Niche (GEN) model is nearly complete. It will allow us to test hypotheses about functional response. The niche model can be refined through experimentation and inference, to represent implicit, non-localized system potentials that drive ecology and evolution. This is in contrast to their current design and use, in which the representation of system potential is confounded with processes of attraction and realization, making the existing models weak tools for any of these purposes.

I propose that this relational informatics design should be rapidly developed for immediate application with existing observing and informatics systems.

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