

COMPLEX ADAPTIVE SYSTEMS: CROSS-SCALE STRUCTURE AND
RESILIENCE

by

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COMPLEX ADAPTIVE SYSTEMS: CROSS-SCALE STRUCTURE AND RESILIENCE

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University of Nebraska, 2018

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This dissertation is focused on scaling and resilience of complex adaptive systems, including ecological and economic systems. In particular it is concerned with the textural discontinuity hypothesis (hereafter called the discontinuity hypothesis), which describes how the distinct spatial and temporal scales of processes that shape systems in turn generates distinct spatial and temporal scales in system structure and entities interacting with that structure; the cross-scale resilience model, which uses the discontinuity hypothesis as the foundation of a theory about specific system features that drive ecological resilience; panarchy and adaptive cycles, which articulate how system dynamics at the above-mentioned scales change over time and how feedbacks across those scales informs system behavior; and the notion of spatial regimes in ecological structure. I both expand existing frameworks to accommodate non-ecological complex systems, and test my hypotheses in a variety of economic and ecological systems.

Some general findings of my analyses are that the objective identification of scale domains in many types of complex systems can be useful for understanding how pattern and process shape structure and impact system-level resilience. Economic systems, for example, as expressed by Gross Domestic Product, fall into distinct, non-random size classes that suggest there are scale-specific processes generating basins of attraction. I expand the cross-scale resilience model to incorporate abundance, a

species and community attribute that is mechanistically related to the provision of function and resilience. The coral reef fish communities of the Hawaiian archipelago were analysed to see if their cross-scale resilience differed amongst coral dominated and macroalgal and turf dominated reefs, with the surprising result that the macroalgal-turf communities were more resilient. In a twist on classic regime shift theory, which typically focuses on temporal shifts within a single ecosystem, I used a novel information theory method to successfully detect spatial boundaries and transition zones between types of ecological systems by using animal community data. Finally, I argue why the adaptive cycle may be a result of endogenous processes in complex adaptive systems, and is not just a convenient metaphor for cycling behavior and dynamics.

DEDICATION

To Sterling, for always thinking I'm smarter than I actually am, and unconditionally supporting me throughout this process.

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PREFACE

“Nature is an endless combination and repetition of a very few laws”

(Ralph Waldo Emerson, *Essay, Lectures and Orations*. London,
William S. Orr and Co. 1851).

It is increasingly recognized that the systems of most interest to humans, including ecosystems, are complex adaptive systems and need to be investigated and understood as such. A well known physics professor once told me that if we can make an airplane fly through the air then we can remedy climate change. It is easy to see now the problems with conflating two categorically different kinds of systems and having the same expectation regarding their behavior, but at the time I could only walk away frustrated by the logical flaw I could feel but not articulate. An airplane is a complicated but non-complex mechanical system where part A + part B + part C = an airplane, and its functioning as such is predictable and reliable. The climate is a complex adaptive system, and by definition is neither predictable nor ‘reliable’ in its long-term behavior.

There is no singular definition of a complex adaptive system (CAS), and given the breadth of system types encompassed by this term this is only appropriate. Within this dissertation, my definition of a CAS changes in emphasis as I navigate from ecological to economic and back again to ecological systems. My primary motivation in this dissertation was to explore some concepts that have as their starting

assumptions the lens of complex adaptive systems. These concepts are part of a collective of ideas that fall under the umbrella of ecological resilience. They are all the brainchild of C.S. Holling and his colleagues, and when viewed as a package operate as a relatively comprehensive framework currently existing for understanding systems as complex adaptive systems. This is not to say that ecological resilience encompasses *all* concepts useful for investigating CAS's—far from it. But it is an appealing framework because of the richness of interconnected ideas that allows a researcher to systematically examine concepts central to ecology, such as scales, stability, and thresholds, with the assumptions of complex adaptive systems theory.

In short, because these concepts will be elaborated at length (and perhaps ad nauseum) in the following chapters this dissertation focused on the following: the textural discontinuity hypothesis (hereafter called the discontinuity hypothesis), which describes how the distinct spatial and temporal scales of processes that shape systems in turn generates distinct spatial and temporal scales in system structure and entities interacting with that structure; the cross-scale resilience model, which uses the discontinuity hypothesis as the foundation of a theory about specific system features that drive ecological resilience; panarchy and adaptive cycles, which articulate how system dynamics at the above-mentioned scales change over time and how feedbacks across those scales informs system behavior; and the notion of spatial regimes in ecological structure (Figure 1).

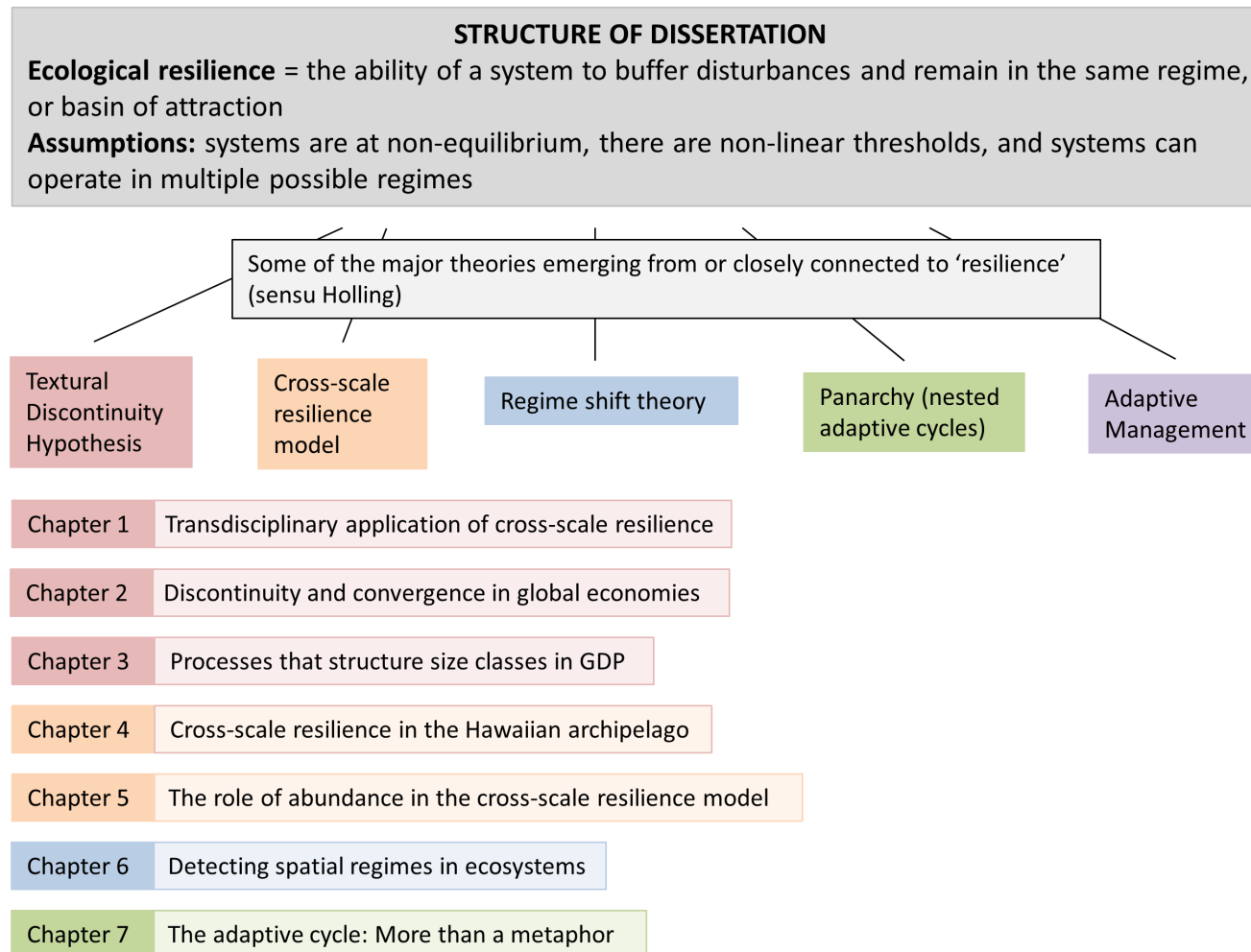


Figure 1 Relationship of dissertation chapters to extended theory of ecological resilience

In Chapter 1, “Transdisciplinary application of cross-scale resilience”, I articulate how the objective identification of scale domains in complex adaptive systems via the discontinuity hypothesis could be utilized in other fields, such as social-ecological resilience, economics, and anthropology. In Chapter 2, “Discontinuity and convergence in global economies”, I apply the discontinuity hypothesis to global cross-national economic systems, using Gross Domestic Product (GDP) to test whether there are scale domains, which can also be understood as basins of attraction, in GDP. In Chapter 3, “Processes that structure size classes in GDP”, I test whether a suite of socio-political-cultural traits associated within economics with GDP are possible explanatory variables/processes for the scale domains found in GDP. In Chapter 4, “Cross-scale resilience in the Hawaiian archipelago”, I compare the cross-scale resilience of coral reef fish communities in the Hawaiian archipelago. In Chapter 5, “The role of abundance in the cross-scale resilience model”, I discuss the implications of expanding the cross-scale resilience model to incorporate abundance. In Chapter 6, “Detecting spatial regimes in ecosystems”, I use Fisher Information to test the location of ecological boundaries (spatial regimes) between ecosystems based on bird community structure, and compare it to the location of boundaries given static eco-region maps traditionally used by agencies, managers, and researchers. In Chapter 7, “The adaptive cycle: More than a metaphor”, I argue that the adaptive cycle and nested adaptive cycles (called a panarchy) may represent endogenous system dynamics of complex adaptive systems as opposed to a useful metaphor for system behavior, and I provide a variety of metrics by which this could be tested. And finally, in the Conclusion, I provide a brief summary of the implications of this body of research.

CHAPTER 1 TRANSDISCIPLINARY APPLICATION OF THE CROSS-SCALE RESILIENCE MODEL

Introduction

Scientists often have a poor understanding of the system-level behavior and dynamics of complex systems, such as ecosystems, economies, or integrated social-ecological-economic systems, whereas they are more likely to have a highly refined understanding of the components of complex systems, such as species or the behavior of individuals in an economy. The essence of a complex system, however, is that its behavior cannot be deduced from simply aggregating knowledge of the components. This fundamental constraint compels the need for tools that allow us to track the impact and consequences of localized changes or disturbances on system-level behavior and dynamics over time and space. The field of resilience science in ecology has studied resilience as an emergent system-level feature of complex ecological and social-ecological systems, and has developed a tool for quantitatively assessing ecosystem resilience, called the cross-scale resilience model. We argue that the cross-scale resilience model can be applied to other types of complex systems.

Once the provenance of ecology (Lovelock 1992), artificial life (Langton 1986), and genetics (Kauffman 1995; Serra et al. 2007), the application of complex adaptive systems theory to new fields has broadened considerably, from health care (data flows and human interactions) (Tan et al. 2005), food and water security (Villa et al. 2014), software development (Batra et al. 2011), business (Mason 2007), legal

systems (Ruhl 2014), medical research (Greek & Hansen 2013), engineered systems such as electrical grids and traffic management (Zhang et al. 2008; Haghnvis & Askin 2012), urban water systems (Kanta & Zechman 2014) and many more. Scientists are embracing a more complex view of system dynamics, and moving beyond long-held assumptions of linear equilibrium behavior for many different types of systems. Understanding universal, or at least broadly applicable, rules of complex systems behavior would assist the challenging task of understanding the ‘wicked problems’ society faces, such as rapid environmental and social change including climate change, economic and socio-cultural challenges, biodiversity loss, and the degradation of social-ecological systems (Vitousek et al. 1997; Millenium Ecosystem Assessment 2005).

Comparative analyses of complex systems have, in fact, demonstrated commonalities among distinctly different types of systems (Schneider & Kay 1994; Holling 2001; Lansing 2003; Foster 2005; Bullmore et al. 2009). Both biological and non-biological complex systems appear to evolve and be structured by similar principles, leading to a limited set of possible topological structures, organization, dynamics and behavior that are to some extent universal across system types (Watts & Strogatz 1998; Gunderson & Holling 2002; Barabási 2009; Bullmore et al. 2009). Levin (1998) proposed that the essential elements of a complex adaptive system (CAS) can be reduced to three elements: “sustained diversity and individuality of components; localized interactions among the components; and an autonomous process, where based on the results of local interactions, a subset of the components is selected for replication or enhancement (p. 432).” From these essential elements flow the other key features of a CAS: adaptation and introduction of novelty (Allen &

Holling 2010), non-equilibrium dynamics as a result of the dispersed and local nature of selection, the absence of top-down global control, and the emergence of hierarchical organization and other emergent phenomena (Levin 1998). Of these features, hierarchical organization and the emergence of resilience is our focus. Resilience is the ability of a system to remain organized around the same set of processes, structures, and functions (Holling 1973).

Within ecology, two parallel avenues of research have examined properties of CASs and their implications for system stability and resilience. The first, network theory, has uncovered rules of topological structure regarding the ways nodes are connected to each other using graph theory (Barabási 2009; Cumming et al. 2010), and examined the extent to which different topologies are resilient to random or targeted node loss (Srinivasan et al. 2007; Dunne & Williams 2009; Uden et al. 2014). In ecosystems, nodes are frequently modelled as species, connected to each other in food webs that generate emergent properties of information storage (such as genetic material), material and energy flow, resilience, and adaptive capacity (Montoya & Solé 2003; Jørgensen & Fath 2004; Pascual & Dunne 2005; Barabási 2009). Network theory has been widely applied to understand the effect of topological properties like connectance on the function and resilience of a broad array of CASs, from the internet, to social systems, and the brain (Barabási 2003, 2007; Pascual & Dunne 2005). However, network theory does not yet account for hierarchy and scaling in a non-arbitrary way when it considers scaling at all. Any scales identified are typically user-defined levels, as in when food-webs are stratified by trophic level (Bascompte et al. 2005).

The second research avenue, that of ecological resilience (Holling 1973), was inspired by the multi-scalar and hierarchical organization of ecological systems. In particular, the discontinuity hypothesis was developed as a mechanistic explanation for the way species' interactions with the hierarchical, scaled nature of their environment structures communities (Holling 1992). The cross-scale resilience model extended the discontinuity hypothesis by providing a testable hypothesis for how system-level resilience can emerge from species' interactions with environmental structures and processes that vary with scale (Peterson et al. 1998). This model has provided one of the few quantitative measures of resilience available to date (Allen et al. 2005; Stow et al. 2007; Angeler et al. 2013a), despite the widespread uptake of the resilience concept. We propose that the cross-scale resilience model may describe fundamental patterns in CASs resulting from dynamics that are general to other types of hierarchical CASs. Here we discuss some of the relevant theory underpinning ecological resilience, the discontinuity hypothesis, and the cross-scale resilience model, discuss recent examples from non-ecological systems, and then propose some systems for which we believe a cross-scale resilience analysis would be fruitful. We expect that a broader application of the cross-scale resilience model to different types of CASs will not only offer possibilities to increase our mechanistic understanding of the organization of ecological, social, and economic systems, but also help provide insight into management and policy challenges under fast-changing environmental and social baselines. Shared principles amongst systems has the pleasing consequence that theory, modeling and tools developed within one field for a particular type of CAS may be pertinent to another field, creating powerful opportunities for shared learning and collaboration.

Resilience

The development of resilience theory has received considerable attention in recent years (Gunderson & Holling 2002; Carpenter & Brock 2004; Folke et al. 2004; Allen et al. 2005; Cumming 2011; Walker & Salt 2012). Ecological resilience is the ability of a system to remain organized around the same set of processes, structures, and functions (Holling 1973). The degree of resilience in a system is a measure of how much disturbance the system can buffer without moving into an alternative regime (Peterson et al. 1998). This is a distinctly different view of resilience than the more traditional engineering resilience, which defines resilience as the return time to equilibrium after a system has experienced a disturbance (Holling & Meffe 1996). Engineering resilience presumes a single steady state, which is at odds with our current understanding of the dynamics of CASSs. In practice, this means that once a CAS has shifted from Regime A to Regime B, an engineering view of resilience would incorrectly assume that the system would eventually rebound to Regime A without substantial intervention. Resilience theory has demonstrated that breaking the feedbacks that maintain the system in Regime B can be very difficult (Scheffer et al. 2001).

Resilience theory is built on an understanding of social-ecological systems as CASSs, thus it assumes non-linear dynamics, and multiple possible basins of attraction governed by different regimes (i.e., different sets of processes). The ability to identify regime thresholds and provide early warnings of regime shifts is a vigorous area of current research (Folke et al. 2004; Biggs et al. 2009; Scheffer et al. 2012). Regime shifts are often abrupt, non-linear transitions between basins of attraction that occur when the threshold for a critical system driver is exceeded. When the resilience of a

system is reduced, systems are more vulnerable to a potential regime shift. Fold-bifurcation threshold dynamics are common in ecological systems, where even a small change in conditions can trigger an abrupt regime shift if a bifurcation threshold is passed, and hysteresis, or the inability of a system to move backward and return to a previous regime, is possible (Scheffer et al. 2001; Scheffer & Carpenter 2003).

Regime shifts in ecosystems epitomize the practical relevance of resilience research because the outcomes of regime shifts are uncertain, and frequently have negative consequences in the form of reduced ecosystem provisioning or increased poverty (Moberg & Folke 1999; Crépin et al. 2012).

The relevance of resilience theory to other types of CASs is possible in part because order and pattern can emerge from the dynamics of self-organization in the absence of natural selection, merely from local interactions between agents (Kauffman 1995). Thus, although natural selection and evolution have corollaries in other fields--businesses as the objects of natural selection, or the evolution of CASs such as civilization, economies, or cities (see (Tainter 1988; Beinhocker 2006), the emergence of higher-order phenomena such as resilience from lower-order localized interactions is not dependent on genetic-based natural selection (van den Bergh 2007). It is increasingly clear that economies and other types of social systems have dynamics more appropriately described by the science of CASs than that of simple, linear dynamics, and tools like the discontinuity hypothesis and the cross-scale resilience model can be used to explore commonalities and differences in the basic dynamics of different types of CASs (Tainter 1988; Beinhocker 2006).

The discontinuity hypothesis

The discontinuity hypothesis describes hierarchy and scaling in ecological systems as a result of structuring processes that occur over limited ranges of spatial and temporal scales. In ecological systems, some processes occur with high frequency and at small spatial scales, while others are slow and operate at large spatial extents, creating hierarchy and heterogeneity. Because the characteristic rate and extent of key structuring processes differ sufficiently, they create scale domains or ranges of scale over which patterns change monotonically or not at all. For example, Wiens (1989) describes the scaling of transpiration, which is regulated by stomatal mechanisms at the scale of a leaf, but by climate at the scale of vegetation regions. Likewise, the processes that regulate the turnover of a pine needle differ fully from those that determine the location and extent of the boreal forest (Holling 1992). Scale domains are separated from each other by a non-linear transition (a discontinuity) to the next set of structuring processes (Wiens 1989; Holling 1992).

The discontinuity hypothesis is based on our understanding that species perceive and interact with their environment at scales that are relative to their body size, and persistence depends in part on how well a species' body mass allows it to take advantage of the resources available at a specific scale (Peters 1983; Holling 1992; Fisher et al. 2011). Animal body mass distributions for a given ecosystem consist of groups of similarly-sized species that exploit resources at similar scales. That is, each body mass group mirrors a specific scale of structure and resource availability in the ecosystem, such that the number of body mass groups indicates the number of scale domains present. These body mass groups are separated by gaps, which reflect a scale break (discontinuity), or transition to a new scale domain.

Countless animal communities have been tested for discontinuities with affirming results (Holling 1992; Havlicek & Carpenter 2001; Lambert 2006; Allen et al. 2006; Nash et al. 2013b).

The discontinuity hypothesis relates to a general problem in ecology and other scientific disciplines regarding the quantification of scale in complex systems in non-arbitrary ways (Gibson et al. 2000; Nash et al. 2014a). There have been few tools available for identifying the fundamental scales present in a system rather than defining levels of organization based on observer bias. Wiens (1989) wrote, “we need non-arbitrary, operational ways of defining and detecting scales” and went on to ask, “How may we recognize domains of scale in a way that avoids arbitrary imposition of preconceived scales or hierarchical levels on natural variation?” The strength of the discontinuity analysis is that it is a tool for identifying the available scales of structure in a system without imposing human preconceptions. There are a variety of methods for detecting discontinuities, such as Bayesian classification and regression trees (BCART), Monte Carlo approaches (such as the Gap Rarity Index), and hierarchical cluster analysis (Allen & Holling 2002; Allen et al. 2005). These methods are used on rank-ordered body mass data for all the species in an ecological community (such as all the birds, mammals, or herpetofauna). Body mass can be obtained from general handbooks, as the patterns of aggregations and discontinuities in a system are highly robust to geographic variation and gender differences in body size (Sundstrom 2009). Alternatively, discontinuities have been found by identifying where the fractal dimension of ecological structure changed abruptly, indicating that different structuring processes are dominant (Li 2000; Nash et al. 2013b). Time series modeling has also been used to identify temporal frequency patterns of groups of

species at multiple scales within aquatic communities, as well as to evaluate aspects of cross-scale resilience, allowing for a more dynamic assessment of the discontinuity hypothesis (Angeler et al. 2010, 2011). All these tools are well established in the ecological literature and are readily applicable to other types of CASs. Once the pattern of aggregations and discontinuities has been identified, then the distribution of key elements thought to generate resilience can be evaluated, as per the cross-scale resilience model (Peterson et al. 1998; Allen et al. 2005; Sundstrom et al. 2012; Angeler & Johnson 2013).

The cross-scale resilience model in ecology

The cross-scale resilience model emphasizes the compartmentalization by scale of the functional traits relevant for the maintenance of ecosystem processes. It posits that the distribution of functional traits within and across spatial and temporal scales in an ecological system is non-random, arises from processes of self-organization (positive interactions between structure, biota and process), and results in system-level resilience. Functional diversity, more so than species diversity, has proven crucial for the persistence and resilience of ecosystems and ecological functions such as primary productivity and pollination over time (Winfree & Kremen 2009; Schmitz 2010; Chillo et al. 2011). Species perform functions such as seed dispersal, pollination, decomposition, and nutrient cycling, and create feedbacks that maintain the ecosystem in a particular regime. The cross-scale resilience model posits that resilience derives from the overlapping but diverse functions within a particular scale domain, and the replication of function across the scales of a system (Peterson et al. 1998). Since disturbances do not affect all scales of a system equally, this pattern of functional distribution buffers the system against disrupted or lost functionality

even if species are lost or reduced in abundance (Peterson et al. 1998; Wardwell et al. 2008; Winfree & Kremen 2009; Sundstrom et al. 2012; Nash et al. 2013b).

Local interactions such as competition should drive species to differentiate in key ways to allow for co-existence (Holt 2009). Species that use similar resources are more likely to co-exist if they take advantage of different scales of resource distribution because this weakens their competitive interaction (Peterson et al. 1998; Ritchie 2009). Species that interact with ecosystem structure at the same scales because of similar body sizes should tend to have a greater fitness if they utilize different resource types. A non-random distribution of species functions is thus a result of species interactions within a discontinuous template. Functional response diversity is also a component of resilience (Elmqvist et al. 2003; Laliberté et al. 2010). Response diversity is the degree to which species respond differently to a shared disturbance (Bellwood et al. 2004). If all species belonging to the same functional group also respond similarly to environmental disturbance, then the response diversity is essentially one. If, however, species in the same functional group are differentially affected by a disturbance, then species less adversely affected can compensate for those species more severely impacted by the disturbance. The distribution of members of the same functional group across the scale domains of a system adds another layer of buffering against disturbances, because disturbances do not affect all scales of a system equally. The cross-scale resilience model proposes that resilience is enhanced when there is a diversity of functional groups within a scale domain, and a redundancy of functional groups across the scale domains, because this pattern will allow the system to absorb and buffer disturbances at a variety of scales due to compensatory dynamics (Wardwell et al. 2008; Sundstrom et

al. 2012). Resilience is thus a consequence, and an emergent property of, complex discontinuous systems.

An example of the cross-scale model in non-ecological systems

Only a small body of work has explicitly extended either the concept of discontinuous scaling in complex systems or the cross-scale model of resilience to non-ecological CASs (Garmestani et al. 2006, 2007, 2008). Researchers applying the discontinuity analysis to city sizes found that the distribution was discontinuous, as city sizes fall into discrete size classes with growth rates that differ at different scales (Garmestani et al. 2007). Discontinuities appear as gaps in rank-size distributions of city size within a region. Even though cities grew or shrunk over time, the overall distribution pattern remained discontinuous, suggesting that the size classes reflect the scales of opportunity available in a given system and the processes that structure city size operate at discrete spatial and temporal scales (Garmestani et al. 2007). In a follow-up to this work, Garcia et al. (2011) analyzed the evolution of this city size distribution calculating Markov transition matrices that show the probability of a city moving up or down a size class or ‘state’. They found that while short-term movements between size classes appears chaotic for the small to mid-sized cities, long-term transition probabilities across all size classes reveals relatively conservative system structure. Furthermore, the most persistent cities were the largest cities in the analysis, which lends further strength to the proposition that urban systems partition into levels in a dynamic hierarchy (Eason & Garmestani 2012).

In another example, Garmestani et al. (2006) examined firm size distributions for manufacturing firms for the state of South Carolina, USA. They demonstrated that industrial sectors are comprised of firms that are clustered in size classes. They

characterized resilience in industrial sectors (Garmestani et al. 2006) by following the cross-scale resilience model of Peterson et al. (1998) and analyzed whether the coefficient of variation in employment trends (a proxy for resilience), was correlated to functional richness within an industrial sector. Functional richness was the number of size classes within an industrial sector, and the distribution of functional groups across the size classes, with functional groups represented by sub-sectors within an industrial sector. They expected that a more resilient industry would have more stable employment trends, and that this resilience would be correlated to having a higher functional diversity spread across more size classes within that industry. They found that manufacturing industries with greater functional richness spread across size classes exhibited less volatility in employment. The ability of small and large firms to adapt to variability in their “environment” without adding or shedding members suggests that economic resilience is enhanced when firms of different sizes emerge or are encouraged to emerge within industries.

Applying the cross-scale resilience model to other complex adaptive systems

There are four assumptions underlying the cross scale resilience model that are germane to other complex systems. We describe those assumptions and their implications using a well-established ecological example (Figure 1). The first assumption is that there are key processes in a complex system (A) that generate scale domains of structure (B) in a system. These scale domains are the “deep structure” of a system. Because the deep structure is scale specific and discontinuous, so too is the distribution of the components (e.g. the organisms in ecological systems, or cities in regional systems) interacting with that structure (C). Resilience (D) emerges from the

way critical functional attributes of these components are distributed across the discontinuous scale domains. Ideally, all these assumptions would be tested to understand CAS dynamics mechanistically, but assessing the processes that create the deep structure is often limited because some processes act over such broad spatial and temporal extents that they are challenging to measure. These limitations make an assessment of (A) difficult. However, determining (B) through (D) allows for the detection of patterns relevant for inferring resilience without the need to understand causal mechanisms. For example, Garmestani et al. (2005, 2006) found that both firm size and city size were reasonable analogues of animal body size, as firms and cities fell into distinct aggregations of similarly-sized firms with scale breaks between size classes, but they did not identify the scale-specific processes that generated the deep structure. Nevertheless, their identification of discontinuities and aggregations in system features such as firm size and city size provided insight into the dynamics of those urban and social systems, and their implications for resilience. This is useful for researchers applying tools across CAS types, because the distribution of key functional elements within and across the system scales should be a signature of emergent resilience (e.g. (Angeler et al. 2012)).

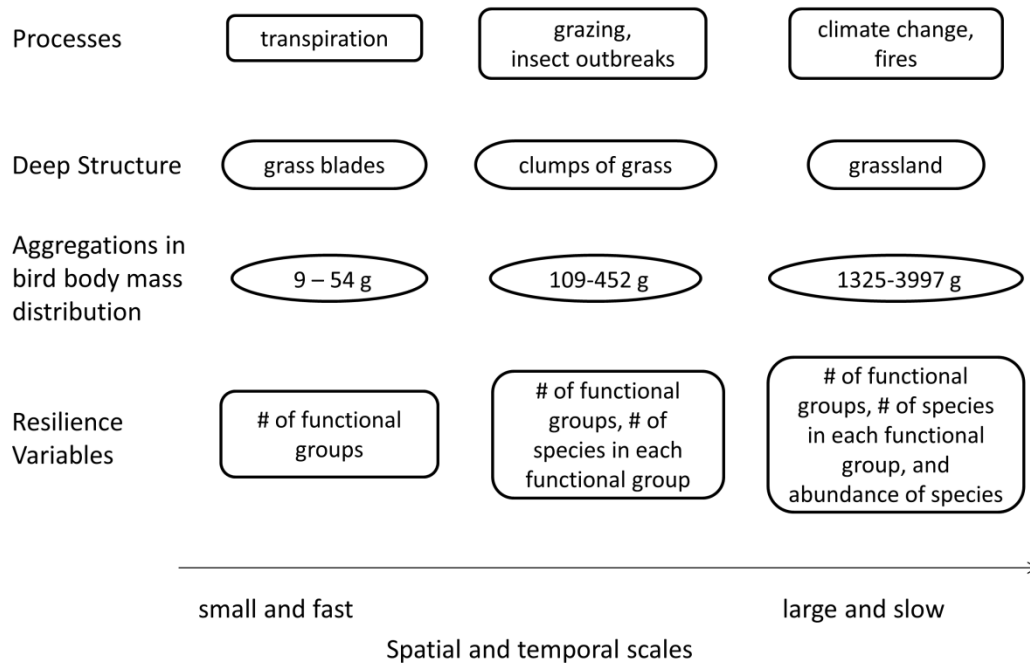


Figure 1.1 Four layers of a cross-scale resilience model using simplified grassland. First, the key processes occur at discrete spatial and temporal scales, creating the heterogeneous and hierarchical scales of deep structure present in the system. Animals interact with the deep structure allometrically with their body size and are more likely to persist if their body mass is congruent with the scales of deep structure present. Resilience emerges from the non-random distribution of functions as performed by species within and across the scales of the system.

Because CASs are capable of existing in multiple different basins of attraction, defined by alternate regimes (Biggs et al. 2009; Scheffer et al. 2012) it is important to understand the resilience attributes associated with each regime (Angeler et al. 2013b). For instance, a lake can exist in a clear-water, oligotrophic regime, and a turbid-water, eutrophic regime. The turbid regime results from excessive nutrient loading and is undesirable because of reduced ecosystem service provisioning. The turbid state can also be resilient, making it extremely difficult to manage back into an oligotrophic regime (Scheffer & Carpenter 2003). Terrorist networks, comprised of

small cells that operate at discrete spatial and temporal scales and with limited cross-scale interactions, are also highly resilient to disruption because of the discontinuous structure of their organization. In both cases, this is not a resilience that is desirable (Bousquet 2012). Understanding what generates resilience, how to quantify it and therefore manage it, is of interest for any CAS upon which humans depend.

Examples include social-ecological systems upon which we depend for food, water, recreation, and other values; our economic systems upon which much human well-being is dependent; socio-political systems which provide the stability to pursue a high-quality life; and the human body, including neurological and other biophysical human sub-systems. We describe the application of the cross-scale resilience model to several types of complex systems below (see also Table 1).

Table 1.1 Examples of types of complex adaptive systems and variables that may be conducive to a cross-scale resilience analysis.

Systems	Variable	Functional Attribute
Social-ecological/Urban Systems	Population size	Emergency services Production Transportation options Employment diversification and evenness Energy grid Food network Types of open spaces Ecosystem services
Socio-cultural Systems	Population size Government size/type	Cultural diversity Educational opportunities (e.g. years of schooling) Socio-economic diversity Political upheaval Size of governed area
Economic Systems	GDP Size classes of industry types within an economy GINI coefficient Stock market indexes	Industry types (product diversity, export diversity) Natural resource dependence Employment (qualifications, redundancy) Standard-of-living measures Market sectors
Socio-historical Systems	Population size	Access to environmental resources Social connectivity within and across scales Type of governance

Social-ecological

The development of resilience theory in the last two decades has occurred almost exclusively within the realm of ecology. Much of the research conducted on ecosystems has treated humans as external to the system, but has developed quantitative methods to assess resilience (such as the cross-scale model) and the

probability of regime shifts (Allen & Holling 2008; Scheffer et al. 2009), while another large body of work dealing explicitly with social-ecological systems has tended to focus on conceptual frameworks and assessments of resilience proxies (Walker et al. 2002; Cumming et al. 2005; Adger et al. 2011). Work focused on social-ecological resilience, could, in some instances, benefit from the quantitative identification of domains of scale, instead of relying on more arbitrary levels of organization within the system of interest. This allows for the specific identification of key processes structuring critical scales, or the distribution of functions or services deemed critical for maintaining social-ecological resilience. For example, Janssen et al. (2007) provide a detailed case study assessment focused on configurations of social-ecological systems that have been resilient on century-time scales, but while they use scales to describe ecological/biological processes, they use ‘levels’ to describe human organization structures. The implication is that scales in human systems are observer-dependent. We argue that while the key processes that constrain and structure human organizational structures are often different from those that structure ecological systems, they are nonetheless likely to be few and operate at discrete spatial and temporal scales.

Work on ecosystem services such as crop pollination (Winfree & Kremen 2009) has shown that the stability of crop pollination is dependent on the response diversity and cross-scale distribution of the regional bee population, but the authors pre-selected 7 scales of analysis, rather than using raw data to determine the scales at which bees interacted with the landscape. Ecosystem services is a highly pertinent research topic given the rates of global land conversion, risks associated with climate change, and trends towards urbanization (Costanza et al. 1997; Millenium Ecosystem

Assessment 2005; Rockström et al. 2009; Ernstson et al. 2010). Objectively identifying the characteristic scales at which particular ecosystem services are distributed and the key processes or variables structuring those services would be of value. Furthermore, almost all ecological work focused on scales only considers spatial scales, by drawing buffers of arbitrary size around the focal phenomenon. This fails to identify the actual scales present, and does not account for a significant portion of the influence of scale—the temporal domain.

Urban systems can be considered a subset of social-ecological systems, as both cities and linked networks of cities are considered CASs (Ernstson et al. 2010). Landscape ecologists have recently tackled regularities and deviations in patterns of development in urban systems, using metrics from hierarchical patch dynamics (Wu et al. 2011). Using the cross-scale resilience model as an alternative method to identify key scales within urban systems would be an interesting validation of the landscape ecology approach. If similar scale domains were identified, the benefit of the cross-scale model is that it allows an evaluation of resilience by assessing how the distribution of key elements within and across those scales may impact urban resilience. Another body of work on urban systems has focused on uncovering universal urban scaling laws that demonstrate how the size of a city scales with demographic, socio-economic and behavioral urban features such as crime rates, rate of innovation, and energy use (Bettencourt et al. 2007, 2010). It is likely that the power-law fit for many of these urban features masks deviations and discontinuities that reflect structuring processes that are not scale-invariant, and would allow researchers to determine why some cities are resilient and persistent over time, as compared with others (Garmestani et al. 2007, 2008). Bettencourt et al. (2010) write,

Scaling laws provide the average baseline behavior and the null-model for addressing how to rank cities meaningfully and assess the effects of local events, historical contingency and policy, independently of population size. . . we show how deviations from scaling laws can be used to construct truly local measures of a city's organization and dynamics.

Ernstson et al. (2010) argue that urban-ecological processes operate at multiple spatial-temporal scales and that cross-scale interactions are key to understanding system-level resilience. We suggest that deviations from scaling laws may not be confined to local contingency, but reflect structuring processes that are scale-specific and general across social-ecological systems, as in the work on human cognition that suggests that people can only meaningfully interact with roughly 150 other people, thus structuring social networks at that scale domain (Aiello & Dunbar 1993; Kosse 2001). Just as the key processes that structure ecological systems are few and occur at characteristic spatio-temporal scales, the processes that structure human social organization appear to be as well (Kosse 1990; Aiello & Dunbar 1993; Dunbar 2008).

An analysis of the rank-ordered distribution of the population of 179 U.S. Bureau of Economic Analysis -defined economic areas within the United States of America shows that there are six distinct size classes within the data set, which ranged from 80,415 to 23,285,781 people (Figure 2). An Economic Area reflects regional markets surrounding metropolitan or micropolitan statistical areas, which are defined based on commuting and newspaper readership data (Johnson & Kort 2004). Size classes were identified using standard methods (Gunderson & Holling 2002; Garmestani et al. 2008), and the number of classes was consistent with regional

distributions analyzed by Garmestani et al. (2005). Time series analysis on this nation-wide BEA data set would allow researchers to examine robustness of size classes over time and the key processes generating the size classes, transitions of regions between size classes, and features of regions that promoted resilience and stability or were destabilizing over time.

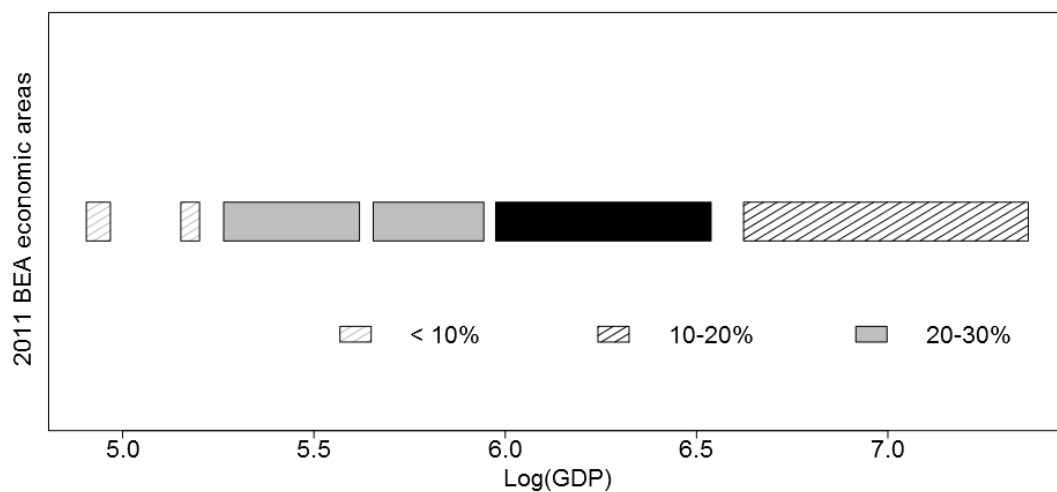


Figure 1.2 Discontinuous distribution of 2011 Bureau of Economic Analysis (BEA)-defined economic regions for the United States of America. Bars represent size classes, while shading indicates what percentage of the 179 BEA regions fall into each size class. Bars are separated from adjacent size classes by significant gaps, or discontinuities.

Archaeology/Anthropology

Human social organization has been explored by archaeologists, anthropologists and social historians from two primary viewpoints: the growth and development of human social organizations at all levels of organization over time, and the collapse of said organizations (Tainter 1988; Diamond 2004). Despite the fact that human social organizations as CASs is widely accepted, few archaeologists have pursued complex systems theory as an avenue for exploring these dynamics of

development and collapse over time (though see (Bettencourt et al. 2007, 2010; Adger et al. 2011)). Interestingly, archaeology has recently embraced many of the basic concepts associated with resilience theory, especially that of the adaptive cycle (Redman 2005; Nelson et al. 2007; Hegmon et al. 2008; Dunning et al. 2012). The adaptive cycle provides a conceptual framework for understanding the dynamics of a system that moves through cycles of accumulation, collapse, and renewal, which were already a central focus in archaeological research. Much of this work, however, is largely descriptive and fails to objectively identify underlying scales of deep structure that might drive system dynamics over time (Uden et al. 2014). Rather, it relies on human organizational levels and uses resilience theory and the adaptive cycle as an extended metaphor for explaining development and collapse dynamics in archaeological data (Dunning et al. 2012; Ekblom 2012). Holling's discontinuity hypothesis was developed as a way to empirically test the adaptive cycle (Holling, personal communication), as it presumes hierarchal, nested, discrete scale domains, much as the cross-scale model was developed as way to empirically test resilience within and across ecological communities. Part of the failure to embrace the adaptive cycle and resilience more rigorously might be a function of the inherently qualitative nature of the concept—without the cross-scale model as a means of testing whether key functional elements and the pattern of their distribution contributes to resilience, there is no recourse but description. One exception has been the work by Nelson et al. (2011), which assessed whether diversity in household-level variables was correlated to resilience. The mixed results of those studies provide an important caveat to the use of the cross-scale model: first, the authors explored only diversity (and not redundancy) and its relationship to resilience, and at only 2 levels of subjectively-

selected human organization (household and village). Second, all variables are not created equally. In other words, although animal body mass and the functions a species provides appear to incorporate many of the most critical elements of system structuring and system resilience, it is unknown what archaeological variables reflect the core processes and functions present in human social systems, and whether the archaeological material culture available to researchers, such as pottery styles, sufficiently represents the key scaling processes structuring human societies. How the basic concepts of diversity and redundancy within and across system scales translate into human material culture is an open question, but the cross-scale model would provide a quantitative platform with which to explore these not insignificant questions.

Scaling in human population size has been treated by archaeology in a variety of ways and at various levels of organization. For the level of early villages, Rappaport (Bandy 2004) developed what he called the ‘Irritation Coefficient’, which described the non-linear scaling relationship between an increase in population size and an increase in sources of irritation, or frequency of disputes. Johnson (1982) dubbed the phenomenon scalar stress, and argued from a social evolution perspective that due to the ‘Irritation Coefficient’, expanding populations will either be forced to fission, and split into smaller and more manageable groups, or a higher-level governing layer capable of mitigating scalar stress will emerge. Though archaeological evidence for fissioning in early villages and/or the emergence of a higher-level of institutional complexity is scarce due to the difficulties of data, scalar stress and its role in structuring scale domains of human population sizes remains a widely accepted theory (Friesen 1999; Bandy 2004; Parkinson 2006). The degree of

acceptance despite the scarcity of hard evidence stems from work done by a wide array of theorists who have demonstrated that a) the location of population size ‘hinge points’, or thresholds, are common across human populations situated in very different environmental and cultural contexts, and b) human cognitive factors such as short-term and long-term memory and limitations in information processing capabilities provide mechanisms for population hinge points (Ember 1963; Kosse 1990, 2001; Dunbar 2008). Subsequent work has shown that while the relationship between size and complexity is in general true, it can break down at narrow demographic ranges, as local context becomes more critical in structuring populations and their complexity (Feinman 2011) and this is congruent with the discontinuity hypothesis. A discontinuity analysis on archaeological data would be revealing of the key scale domains within which human populations fall, particularly as it uses raw data while previous work on archaeological data has used binned data, which can muddy the ability to find break points or clusters in rank-ordered data (Kosse 1990; Feinman 2011). If human population sizes are structured by key processes operating at discrete spatial and temporal scales as Kosse (2001) and others have suggested (Dunbar 2008), then a resilience assessment could be conducted using the complexity variables already well established in the archaeological literature (Feinman 2011). Resilience could be synonymous, for example, with locational persistence at a comparable complexity, and its correlation with diversity and redundancy of environmental resources or social networks, or any other factors deemed critical for long-term persistence could be tested. If a discontinuity analysis detected similar aggregations of population sizes across disparate environments and cultures, this would indicate that the processes scaling populations are general to all humans, which

would suggest that they are based on conservative patterns in primate evolution. An alternative is that some scales of aggregation are structured by primate evolution, while others may be more contingent on regional context, be it environmental or social, that nonetheless ought to be persistent and characteristic across types of environmental constraints or human political organization (e.g. collective leadership versus autocratic leadership) (Feinman 2011). If basic scaling processes can be associated with human population size classes, then comparative studies can begin assessing the degrees of resilience of various communities.

Economic

Since the Great Depression of the 1930s and the subsequent Keynesian Revolution, economics as a profession has been divided into two separate disciplines, microeconomics and macroeconomics. While the former studies micro fundamentals such as the specific market interactions of individuals and firms, the latter focuses on aggregates such as employment, interest rates, gross domestic product (GDP) and their fluctuations. Both the failure of macroeconomics to incorporate micro behavior, and conversely, the assumptions made when macro models do incorporate micro fundamentals has resulted in heated debates over the years (e.g. (Hoover 2012)). The micro-macro divide persists, to the point that most economists define themselves as one or the other. The inability of economics as a science to bridge the two distinct but interacting scales of behavior and dynamics underlines a need for alternative approaches.

Complex systems science has been slow to permeate economics, and despite recent progress (Krugman 1996; Foster 2005, 2006; Beinhocker 2006; Foxon et al. 2013), the study of economies as CASs has remained at the fringes of economics.

Joseph Schumpeter (1934) was one of the few economists in the early 20th century who tried to understand the economy through a complex systems lens, but his ideas, emphasizing the dynamic nature of capitalist societies and business and economic cycles as endogenous behavior, have never been considered part of the mainstream. Schelling (1978) contributed to our understanding of self-organization in space, but less is known about temporal self-organization, such as the causes of the business cycles. Neoclassical economics, the predominant school of thought in economics for over a century, emphasizes economies as equilibrium systems with linear dynamics (Foster 2006), which is an inappropriate characterization for economic systems over meaningful time scales (Arthur 1999; Foster 2005; Beinhocker 2006). That economies are examples of CASs has been convincingly argued (Foster 2005, 2006; Foxon et al. 2013); we extend that characterization by arguing that socio-economic systems can be usefully analyzed from the perspective of discontinuous, hierarchical scales of structure, and the emergence of resilience from the distribution of key elements within and across the scales of a system.

Growth dynamics in economies appears to parallel those of ecosystems, suggesting that the evolutionary processes at work in both CASs are similar. Ecosystems and economies tend to increase in complexity over time, as they evolve increasingly complex structures to dissipate greater amounts of energy (Schneider & Kay 1994; Beinhocker 2006). Stability or persistence over time occurs because of positive and negative feedback loops that reinforce processes of self-organization. A primary feature of stability in CASs comes from the trade-off between diversity and redundancy, rather than from the maximization or optimization of efficiency by maximizing diversity (Loreau 2010; Page 2010a). Increased diversity provides

adaptive capacity because for evolution to occur systems must be able to change structurally in response to selective pressures (Foster 2005), while redundancies provide a greater ability to withstand the loss of any one entity in the system (Peterson et al. 1998; Page 2010a). Maximizing efficiency is destabilizing at the system level, as redundancies are critical in order to buffer disturbances. Lee et al. (1998) found that though larger economies tended to be more diversified and thus have smaller relative fluctuations in growth, they were less diversified than would be expected if diversity increased linearly with size.

If size of economy is a key variable reflecting the scaling processes in economies, then the size distribution of economies should be discontinuous, reflecting the key scales of structuring processes. A cross-scale analysis of economies is predicted to confirm that the distribution of diversity within and across the scales of the system should be non-random, and those economies with increased diversity within scales and greater redundancies across scales ought to have greater resilience than less diversified economies. Guilmi et al. (2003) found GDP per capita for countries between the 30th and 85th percentile fit a power law, suggesting that there are multiple scales of structuring processes in order to explain the tails of the distribution. Hidalgo and Hausman (2009) examined the economic complexity of nations from a network perspective, moving away from traditional geographic or institutional explanations of economic growth. They focused on how the diversity of a country's labor inputs and the degree to which their exports are non-ubiquitous positively correlates with higher GDP, as well as being a good predictor of future GDP growth, demonstrating the importance of analyses that depart from a singular focus on system growth measures towards approaches that consider indicators of

system resilience, and challenging classical theories on comparative advantage in economic development (e.g. (Leamer 1984).

Ormerod (2010) examined the resilience of capitalist economies to recessions, defining resilience as the duration of a recession, and found that capitalist economies were surprisingly resilient. Though this definition of resilience falls into the engineering category, presuming a single equilibrium state, it is one of the few to explicitly analyze how rapidly an economy is able to reorganize and rebound. He found that more than two-thirds of all recessions in the last 140 years lasted only a single year, regardless of the initial size of the recession. As there were a wide range of policy reactions to the 255 recessions, Ormerod (2010) postulated that resilience to recessions is an inherent feature of economies, though without offering suggestions as to what structural features or mechanisms of a capitalist economy buffer the disturbance effects of a recession. The data did not fit a power-law, allowing us to reject the possibility that the probability of recessions is scale-invariant, and inviting the possibility that the cross-scale model could provide a method for probing the cross-scale characteristics contributing to economic resilience.

Tests of the cross-scale model

Applying the cross-scale model to non-ecological systems requires data that can be rank-ordered and is assumed to reflect key scaling processes, such as animal body masses in ecological systems, city sizes in a region, or firm sizes in an industrial sector (see Table 1 for examples). The data can be analyzed for discontinuities using one of several methods previously discussed (i.e. BCART, GRI, cluster analysis, fractal dimension, or time series analysis). The distribution of functionality within and across the scale domains identified in the discontinuity analysis is proposed to

directly affect system-level resilience, so the data also needs to have a functional attribute associated with it. In ecological systems, this is represented by species' functional traits, while in economies it might be the diversification of sectors contributing to GDP, or in anthropological studies the diversity of food resources available to populations. The next step is to analyze the distribution of functional attributes within and across the scale domains identified (Wardwell et al. 2008; Sundstrom et al. 2012; Angeler et al. 2013a). Are the functions non-randomly distributed? Finally, the distribution pattern of function needs to be related to some measure of resilience, such as employment volatility (Garmestani et al. 2006), regime shifts in ecological systems (Scheffer et al. 2001), or socio-political upheavals (Karunanithi et al. 2011). We have outline some systems that could be explored in this way, with examples of variables that can be rank-ordered, and functional attributes associated with those variables that can be analyzed for a measure of resilience (Table 1).

Conclusions

Biota, including humans, interact with the environment at distinct scales and create self-reinforcing patterns resistant to disturbance (Peterson 2002). The multiple but distinct scales of self-organization and the distribution of function within and across scales generates system-level resilience (Peterson et al. 1998). Thus, a system's resilience is dependent upon the interactions between structure and dynamics at multiple scales.

Science has historically assessed complex systems in a reductionist fashion, decomposing the system into its constituent parts and attempting to understand and define the mechanisms driving each part. While the knowledge gained about the

individual parts of the system has been invaluable, it has not led to the hoped-for insights into managing the system as a whole. Complex systems science has sought to address this by uncovering the general rules of behavior governing complex systems, rules that are not adducible from examining the constituents of the system. If resilience to disturbances is an emergent phenomenon of complex systems beyond ecosystems, then research into the key variables driving resilience provides an avenue for research tracking changes in resilience over time, conducting comparative analyses of resilience between systems, or as means of identifying critical variables on which policy and management actions should focus. The cross-scale resilience model provides a method for non-normative, quantitative assessments of resilience, and is, to our knowledge, one of the only methods available for doing so.

Our ability to identify and measure the key cross-scale variables that contribute to resilience provides society more options for choosing what system state is most desirable, and to successfully manage the system to remain in that particular regime. The increasing risk of concatenated crises suggests an urgency for doing so (Biggs et al. 2011). Just as network theory has contributed to our understanding of how network structure shapes a networks' resilience to loss of nodes (Dunne et al. 2002), so does the cross-scale resilience model contribute to our understanding of how the spatial and temporal distribution of key system variables buffers a system against disturbance and loss of species (Peterson et al. 1998). It is critical that we allocate our management resources towards system components and dynamics that underpin the fundamental resilience or behavior of the system, as opposed to identifying management targets based on subjective or reductionist views of what 'matters' in the system.

The application of these concepts to other types of systems is in its infancy, though work on the distribution of firm sizes and their ‘functional’ role strongly suggests that similar processes are at work in structuring key patterns in economic systems. Many systems not discussed here would be conducive to a cross-scale resilience analysis, such as those found in neurology, immunology, physiology, microbiology (virology and bacteriology, as well as relationships with human health), paleo-ecology (e.g. diatoms), evolution, and political science. Many questions remain, but testing the cross-scale resilience model on these varied systems could lead to significant breakthroughs.

CHAPTER 2 DISCONTINUITY AND CONVERGENCE IN GLOBAL ECONOMIES

Introduction

The application of complex systems theory to economics has been a recent endeavour relative to uptake by other fields. Most economists have not embraced a complex systems approach despite a push from within the field arguing that economies are complex adaptive systems and ought to be studied as such (Anderson et al. 1988; Arthur 1999; Foster 2005, 2006; Beinhocker 2006; Kirman 2010; Foxon et al. 2013). J. Doyne Farmer (2012) commented on the irony given that “the goal of a complex systems focus is to characterize emergent phenomena . . . and Adam Smith is widely regarded as the first to clearly articulate the concept of an emergent phenomena”. Durlauf (2005) justified this slow uptake by arguing that the complex systems models often do not embody “fundamental features of financial markets”, fail to produce economic insights, and do not make a sensible mechanistic connection to economic processes. These are legitimate arguments, but do not negate the need for basic research into the fundamental patterns and processes shaping economic systems as complex systems, rather than continuing to assume variations of linear, equilibrium behaviour.

A premise of complex systems science is that different types of systems can share basic principles of dynamics and behaviour (Foster 2005), which allows for the possibility of interdisciplinary cross-fertilization (Sundstrom et al. 2014). We take

advantage of research and theory originating primarily from ecology to search for patterns in global economies over time. Complex systems are multi-scaled and hierarchical, and the scales in a particular system can be objectively identified (Angeler et al. 2015a). They are fundamental to the system and not arbitrarily defined levels of organization (Wiens 1989; Holling 1992). The scales present in a given system result from both system and scale-specific processes that persistently operate at limited spatial and temporal scales, creating scale domains, or ‘regions where pattern does not change or changes monotonically with changes in scale’ (Wiens 1989), and they provide the basic structure around which other organization develops. They also dictate interaction strengths among system elements, as elements operating at widely disparate scales are likely to have weaker interaction strengths than those operating at similar scales. Some processes, such as competition, niche market exploitation, or cognitive factors that structure short- and long-term memory and limit information processing capabilities (Ember 1963; Kosse 1990; Dunbar 2008), may operate across all scales, but may not operate in the same way across all scales, further contributing to the creation of persistent scale domains. Evidence of multi-scaled structure in economies has implications for system-level behaviour and dynamics that are of value to economics because it has direct bearing on our ability to understand the key processes structuring scale domains (analogous to size classes) in Gross Domestic Product (GDP), and therefore the ability of countries to transition between scale domains.

This paper tests whether there are multiple scales in the global economy, or more precisely, whether cross-national economies are discontinuously distributed. We also determine if the discontinuous distributions identified are conservative over

time. As there is considerable overlap between this and the literature on convergence clubs (Barro & Sala-i-Martin 1992; Quah 1996a; Durlauf et al. 2005; Phillips & Sul 2007), we begin with a review in Section 2 of the convergence club literature, which evaluates countries or regions to determine if they share a similar rate of a particular econometric such as growth, or appear to be converging toward a similar rate.

Although our research is complementary to the convergence club literature, it is grounded in different assumptions about system dynamics and behavior, so in Section 3 we review the theoretical assumptions of complex systems theory and discontinuities as it applies to our analysis. In Section 4 we describe the methods used to identify discontinuities as well as the multivariate analyses we used to expand our interpretation of the results. In Section 5 we describe the results, and in Section 6 we discuss the implications of the results as they pertain to global patterns in GDP, the convergence club literature, and processes that may structure GDP over time. We conclude in Section 7 with a summary of the relevance of the analyses.

Economic convergence clubs

Disparities in wealth and growth between rich and poor countries has been an area of intense research, and is the focus of a vast literature on convergence clubs (see Durlauf et al., 2005 for review). Early work on convergence clubs focused on a null hypothesis of β -convergence amongst all economies in their per capita income due to differing growth rates (Barro & Sala-i-Martin 1992) and was evaluated using linear non-stochastic growth models based on Solow (1956). Convergence to a steady state could be absolute, or conditional on controlling for differences in ‘conditioning’ variables (Mankiw et al. 1992). Since then, research has focused on identifying convergence clubs, or subgroups of economies or regions with similar initial

conditions that seem to converge to a similar growth rate, and then trying to identify univariate factors correlated with club formation, such as human capital, technology, openness, and fixed capital investment. New methods now include convergence in non-growth variables such as financial metrics (Phillips & Sul 2007; Apergis et al. 2012), as well as the consideration of multivariate analyses of factors correlated with club formation and membership (Battisti & Parmeter 2013). Despite substantial methodological developments, El-Gamal and Ryu (2013) state, “the primary conclusion of this massive literature has been rejection of the global convergence hypothesis, based on evidence of multi-modality or other measures of polarization”.

Our interest in convergence clubs lies in identifying the intersections between convergence clubs and that of complex systems science and the discontinuity hypothesis. Kurakin (2009) wrote of molecular biology, a field undergoing a similar paradigm shift to that of economics, “the transition from the old image of biological organization to a new one resembles a gestalt switch in perception, meaning that the vast majority of existing data is not challenged or discarded but rather reinterpreted and rearranged into an alternate systemic perception of reality”. Although much of the convergence club literature interprets its findings primarily through variations of a neoclassical lens, we focus on the convergence research that has moved beyond expectations of equilibrium and linear dynamics to more varied, non-linear, stochastic, and non-equilibrium dynamics. In fact, the consistent finding of more than one convergence club is itself suggestive of these more complex dynamics. The evolution of the convergence literature away from the linear equilibrium dynamics of neoclassical economics has occurred in multiple ways detailed in the following list.

1. Initial conditions

The importance of initial conditions, history, and path dependence has been explicitly incorporated into models to varying degrees, and its importance to long-run economic behaviour is generally acknowledged (Nunn 2009), but often has simply manifested in confining groupings of countries to those with similar initial conditions in accordance with the definition of convergence clubs by Durlauf and Johnson (1995) (as in (Baumol 1986), but see (Owen et al. 2009)). This becomes problematic when researchers consider clubs to be interchangeable with multiple steady states, multiple equilibria, and basins of attraction. The literature appears to have adopted terminology but not content from dynamical systems research, as there are no such definitional restrictions regarding the dynamics of attractors and basins of attraction. A fixed point attractor can pull in systems from widely varying initial positions, a strange attractor can push apart two systems that begin close together, and a single steady state system has no basin of attraction because all points begin and end at the same place (Kauffman 1993). It is unclear why researchers have constrained their modelling assumptions in such a way when the type of attractors operating in economic systems is largely unknown. Likewise, acknowledging that initial conditions are relevant to the current state of economies, but then assuming that the arbitrary start year of their data set contains the necessary initial condition, casts doubt on the fundamental (non-observer defined) nature of the clubs thus identified. Finally, path dependence via history are important to dynamics over time for reasons beyond initial conditions, and these are rarely if ever incorporated into growth models (Beinhocker 2006) (though see Nunn, 2009).

2. Constraints on results resulting from theoretical and methodological assumptions

More studies are allowing for the possibility of multiple clubs, and some are allowing the number of convergence clubs to emerge from the data, rather than being *a priori* selected (Desdoigts 1999; Huang 2005; Owen et al. 2009; Di Vaio & Enflo 2011). However, the sample size varies widely and ranges from the teens to close to the full complement of countries, so the ability to detect clubs and the number of clubs represented by the data varies widely, making generalized conclusions difficult (Alfo et al. 2008). Despite the finding of multiple clubs, most methods cannot distinguish between multiple equilibria that are transient states reflecting different initial starting positions along a singular trajectory towards one long-run equilibrium, or actual alternative states (Durlauf et al. 2009; Owen et al. 2009; Galor 2010a). It is not uncommon for researchers to describe these multiple equilibria as being stationary (Azariadis & Drazen 1990), which suggests an expectation for long-term growth behaviour akin to a fixed point attractor and single point equilibrium dynamics (though see El-Gamal and Ryu, 2013). Although there has also been a partial shift within economics from expectations of non-stochastic equilibrium to alternative ideas of stochasticity, deterministic chaos, non-linearity, and non-equilibrium dynamics, it has been sporadic. For example, in Phillips and Sul (2009), neoclassical expectations of homogenous technology and global convergence are relaxed to allow for heterogeneous technological progress and the possibility of global convergence to a steady state (among other possibilities), but the definition of global convergence is one in which ‘all countries are growing’, which is a rather different proposition than one which requires that all countries converge on a similar growth rate. In a review of

the literature, Apergi et al. (2012) write, “The actual data confront researchers with the fact that real income per capita diverges across all countries. What remains unclear is what factors prevent incomes from converging”, which assumes that there is one underlying fixed-point attractor. We suggest that multiple convergence clubs may be an inherent and fundamental feature of complex adaptive systems (CAS’s). Some researchers have moved away from testing convergence clubs *per se*, and are asking more fundamental questions about the existence of multiple regimes in economies (Di Vaio & Enflo 2011; Cao et al. 2014). This is a promising development as it denotes basic theory building about fundamental assumptions.

3. Treatment of growth

Growth is increasingly treated as heterogeneous in both rate and time to convergence (Maddala & Wu 2000), and is usually treated as endogenously generated rather than the result of exogenous technical progress. Some modelling techniques can capture heterogeneities in control variables, and not just the growth term (Di Vaio & Enflo 2011). We suggest that the separation of endogenous and exogenous drivers is a matter of observer scale and the boundary of the system in question rather than a true distinction between external and internal drivers. As economist John Sterman wrote, “(Almost) nothing is exogenous” (2002). The consequences from the perspective of theory, modelling, and implications of results is far from a matter of semantics, because Solowian growth models which view growth as exogenously driven are constrained in how far they can be adapted to internalize what were once considered externalities (Beinhocker 2006). Endogenous growth models allow growth to be generated from processes of self-organization and internal system features, thus are more appropriate for modelling CAS’s. Whether or not shared

growth rates are a key process forming the multiple equilibria/basins of attraction/scale domains of the global system is a highly non-trivial question.

4. Assumptions around modality and basins of attraction

Where researchers allow for multiple modes, they are finding more than bimodality for a wide variety of econometrics (Durlauf & Johnson 1995; Apergis et al. 2012), including relatively stable and persistent clusters of rich and poor countries but also an intermediate group of countries which are less stable and more dynamic (Battisti & Parmeter 2013; El-Gamal & Ryu 2013). If the clusters identified represent basins of attraction as is often assumed in the convergence literature, then dynamical systems theory suggests that basins in the messy middle range are not of equal size or stability relative to those in the tails. Basins can be transient and/or shallow, blipping in and out of existence as the terrain of the state space changes shape (Kauffman 1993). This is not recognized by the convergence club literature, however, which tends to assume that a basin must be static to qualify as a basin (Galor 2010a; Pittau et al. 2010). A system can move from one basin of attraction to another due to a small disturbance given the right conditions, and does not necessarily require large shocks as many researchers suppose (Nunn 2009; Pittau et al. 2010) (though see Bloom et al., 2003). Galor (2010a), like others, presumes that large exogenous shocks are required to overcome thresholds in poor convergence clubs and therefore discounts the very notion of thresholds because it does not account for how once poor countries that are now rich overcame the threshold in the absence of a large shock. This is a strawman argument, as endogenous dynamics can move a system near to a threshold, reducing the size of shock necessary to surmount it. Likewise, the height of the threshold between basins is dynamic in response to drivers that can change both the state space

within which the basin is embedded, or the dimensions of the basin itself. This is not to say that movement directly from any one attractor to any other is possible; movement is thought to be limited to a few neighbouring attractors, from which further perturbations can push the system to yet others (Kauffman 1995). But presuming that movement between basins requires a large exogenous shock is not supported by theory or data from systems research (Scheffer et al. 2001). In a particularly egregious miscomprehension of CAS dynamics, Nunn (2009) argues against the presence of multiple equilibria in economic systems because of examples such as cities that experience severe disturbances such as the bombings of WWII, but quickly return to their pre-bombing populations, when it is system resilience, or the size of the basin of attraction, that denotes the size of shock necessary or capable of moving a system into another basin (Holling 1973; Scheffer & Carpenter 2003; Fletcher & Hilbert 2007). Finally, assuming that economies fall into only two or three clubs defined by immobility closes the door to the implications of the dynamism inherent to a state space and basins of attraction.

5. Univariate versus multivariate explanatory models

Correlates of growth are beginning to be evaluated using multivariate models which more closely resemble economic reality than do univariate models (Desdoigts 1999; Alfo et al. 2008; Battisti & Parmeter 2013). Multivariate models allow the possibility of assessing the role of multiple variables and their interactions on club formation and membership. It is likely that there are a few key variables for each convergence club that are crucial (Pittau et al. 2010). Battisti and Parmeter (2013) argue, “Given the multivariate nature of the clusters these results suggest something more complex than solely income divergence. The key implication is that the clusters

are diverging across their entire constitution: output, human capital accumulation, physical capital accumulation, and total factor productivity”.

6. Growth rate and threshold behavior

More researchers are considering the possibility of threshold behaviour, which is a characteristic of non-linear dynamics and alternative regimes. Researchers have found that thresholds in human capital accumulation, technology, initial per capita GDP, and literacy, among others, are correlated to multiple equilibria in growth rates (Azariadis & Drazen 1990; Hansen 2000; Huang 2005). For many of the reasons already articulated (widely varying methods, definitions, and data sets) generalizations of results are difficult, beyond the basic conclusion that countries are not all following the same growth path, and there appear to be thresholds in the correlative relationship between various econometrics and growth regime. These studies assume that growth is an appropriate process by which to define convergence clubs, and that may be so, given the goals of the convergence club research. However, if one asks a more fundamental question regarding the presence of multiple basins of attraction and the key processes governing them, growth may or may not be a defining characteristic of any or all basins, and a threshold response does not necessarily denote an alternative basin of attraction as a system can respond sharply to a varying factor without having alternative basins (or multiple equilibria) (Scheffer 2009a). Adjustable rates of processes are a primary mechanism by which complex adaptive systems self-organize to remain in the same basin and adapt to the dynamism inherent in any CAS (Kurakin 2009). For example, businesses do not manufacture their products at one fixed rate, but must adjust to accommodate the changing landscape of the economy they operate within.

The premise of much of the convergence club literature has been that rate of growth acts as an attractor, and that countries with similar initial conditions will converge to a similar rate of growth within a shared basin of attraction. When dealing with an emergent phenomena such as growth rate, Harper (2012) argues that “the goal is to find a set of rules sufficient to generate robustly and replicably the emergent phenomena of interest”. The convergence club literature has failed to find robust or replicable patterns in the number or membership of clubs (for example, see Fève & Pen, 2000), given differences in the timespan of the data, the sample size, and analytical method, aside from consistent evidence that the rich and poor are governed by different processes and different rates of growth. This result is also consistent with the extensive literature on growth in city sizes, which has shown that growth rate can vary based on city size (Garmestani et al. 2007). This suggests that there are scaling processes at work among economies, but that growth rate may not be the best metric by which to identify those fundamental scales.

Growth rates may have more to do with movement from one aggregation or basin to another, either via a threshold effect, past which an economy can transition into a new regime or convergence club, or as a process acting in conjunction with others that allow the transition to another aggregation/club/basin. Whether those groupings are defined by a shared or converging growth rate, or other factors such as openness, technology, human capital, or a country’s product space (Hidalgo et al. 2007) remains to be seen. Galor (2010a) makes the point that for countries that switched to a mode of sustained growth, they did so despite having varying levels of per capita income---rather, it was a critical rate that allowed them to transition (technological progress, population growth, human capital formation). Work on

growth rates and discontinuities in city sizes found that the smallest cities had higher than average growth rates and the largest cities had lower than average growth, so while growth rate was correlated to a city's location on the size spectrum, a similar growth rate was not shared by all cities in the same aggregation so was unlikely to be a central process defining each aggregation (Garmestani et al. 2007). Finally, the use of growth should be carefully evaluated as a defining characteristic is that there are different kinds of growth. There is finite physical growth in the amount of thermodynamic energy mobilized by an economy; theoretically infinite economic growth in money flows, incomes, value added, and expenditure; and growth in human welfare (Ekins 2009). From which derive stability, persistence, and resilience? Convergence in growth concurrently with globalization is a fairly recent phenomenon and seems to be restricted to industrialized countries, whereas poorer countries have witnessed divergence in growth (Epstein et al. 2003; Huang 2005; Di Vaio & Enflo 2011), which suggests, at a minimum, that different basins of attraction are governed by different key processes (Cao et al. 2014).

Complex adaptive systems

There is no singular definition of a complex system, nor should there be. There are, however, working definitions that are sufficiently general to apply to most types of complex systems, as well as sufficiently detailed to be useful. Foster defines a complex economic system in two layers, which serves our purposes and does not fundamentally differ from the definitions proposed by Foxon (Foxon et al. 2013) or Beinhocker (2006). In their most basic sense, complex systems are “dissipative structures that import free energy and export entropy in a way that enables them to self-organize their structural content and configuration, subject to boundary limits. At

the same time, they are open systems irrevocably connected to an environment that contains other systems” (Foster 2005). He proceeds to define complex *adaptive* systems (CAS) in terms of human agency and learning, arguing that an economic CAS would have the following four properties: 1. It contains dissipative structures that transform energy into work and converts information into knowledge; 2. Each CAS is a whole unto itself, as well as a part of some systems and oppositional to others, allowing the emergence of organized complexity at multiple scales; 3. It has a degree of structural irreversibility owing to the inherent hierarchical structure which results in inflexibility and maladaptiveness; and 4. Evolution is temporal, therefore history matters. Phases of emergence, growth, stationarity, and transition result in the generation of variety, innovation, selection, and maintenance (Foster 2005). He argues that a network approach is an ideal way to analyse economic CAS’s because it obviates the substantial problems with constrained optimization, which lies at the heart of modern economic analysis, because network theory is focused on the connections between elements, not the elements themselves (Foster 2005). While we do not disagree with the immense value of network approaches in understanding flows and dynamics in CAS’s as a function of topology and connections, network theory is often focused on scale-free system features, and cannot explicitly account for the multi-scalar, hierarchical structure that intermediates the strength of the connections between components of a CAS, and between other CAS’s.

Complex systems are by definition hierarchical and modular, but there have been few tools available for the objective identification of the fundamental scales of structure. Typically researchers define arbitrary levels of observation based on observer bias. In this paper, we borrow from theory developed in ecology to

understand how scaling impacts the structural features of complex systems. These ideas are formally grounded in complex systems theory, which postulates that system structure consists of multi-scaled hierarchies emerging from processes of self-organization which emerge to dissipate energy gradients (Schneider & Kay 1994; Beinhocker 2006). Other critical assumptions besides emergent phenomena are that economies, as CAS's, operate far from equilibrium; history and initial conditions matter; there are multiple alternative regimes that an economy can reside in and membership in a particular regime is not immutable; many, if not all processes and patterns are defined by non-linearities; and whether or not a process is viewed as endogenous or exogenous largely depends on the scale of observation. These assumptions stand in contrast to that of much of economic theory and literature, including that of convergence clubs.

The ecological perspective

Scaling issues have long been a thorny issue in ecology, yet are of central importance (Levin 1992). It has been tackled by some of ecology's most eminent researchers for more than a century, yet one such researcher lamented relatively recently that, "we need non-arbitrary, operational ways of defining and detecting scales . . . how may we recognize scales in a way that avoids arbitrary imposition of preconceived scales or hierarchical levels?" (Wiens 1989). For the same reason that economists are concerned with explaining how the behaviour of individuals explains that of the economy, so have ecologists tried to understand how the behaviour of individuals explains or predicts that of an ecosystem. The short answer is that it does not, nor cannot. Aggregate behaviour at one level of organization, such as that of an individual, does not typically explain behaviour at a higher level of organization. The

non-linearities in complex system dynamics is both a fundamental challenge of understanding scaling in complex systems, and a gift, because it is not always necessary to understand the behaviour of individuals in exquisite detail in order to model the behaviour of the system. System-level behaviour *emerges* from an incalculable number of individual interactions and is more than the aggregate of those interactions, yet it is constrained by biophysical limits; it will never be fully knowable or predictable over long time spans, but the probable behaviour can be modelled based on an understanding of the scales at which key interactions, processes, and non-linearities occur.

Scaling is of central importance to the understanding of any complex system. The processes that structure any given system do not operate equally across all spatial and temporal scales, and the entities that operate within the system do not interact with each other, structure, or processes equally. For example, small-scale produce farmers who sell their crops at local farmers markets are unlikely to directly interact with food conglomerates that do billions of dollars annually. The local farmer operates at spatial and temporal scales that are magnitudes of order smaller than that of the conglomerate. Explicitly recognizing that scales are inherent to complex systems, that behaviour witnessed at one scale may be less relevant at another, and that patterns observed at one scale domain may disappear when viewed from smaller or larger scales, is critical. Unfortunately, the identification of relevant scales tends to be observer-biased, selected *a priori*, and confounded with levels of organization or aggregation. We recognize the necessity of constraining the scope and scale of any study, as no singular study can encompass all spatial and temporal scales. However, if the choice of scales is arbitrary, then researchers should recognize that any observed

patterns may be random or a function of the scale selection, rather than reflecting actual system patterns and behaviour.

In recent decades, seminal work (O'Neill et al. 1986; Allen & Starr 1988; Wiens 1989) has demonstrated that many ecological processes occur over a limited range of spatial and temporal scales (termed a scale domain) and that even within smooth gradients of process there can be tipping points or non-linearities in the response of structure to thresholds in process (Diez & Pulliam 2007; Yarrow & Salthe 2008). Holling (1992) proposed that if key processes operate over discrete ranges of scale with sufficient persistence over time, then ecological structure should reflect those scalar patterns. Structure that occurs at limited but persistent ranges of spatial and temporal scales should comprise spatial and temporal domains of opportunity for the species that interact with that structure, and be reflected in animal physiology and behavior (Peters 1983; Wiens 1989; Holling 1992). In short, processes that persistently operate at discrete ranges of spatial and temporal scales generate basins of attraction that shape both ecological structure (e.g. vegetation) and animal species. In other words, there are size classes in both ecological structure and animal physiology because key processes that structure ecosystems are not scale invariant.

Researchers have confirmed that animal body mass distributions and ecological structure have a non-random discontinuous structure (Krummel et al. 1987; Holling 1992; Allen et al. 2006; Nash et al. 2013b, 2014a). When rank-ordered body mass data is analysed, animal body mass falls into groups of similarly-sized species, separated by gaps. There are ranges of body mass over which animal species are present, and gaps that reflect the non-linear transition to the next scale domain of pattern and process. This aggregation/gap structure is therefore discontinuous.

Within the gaps, structuring processes are so variable as to not generate any pattern; therefore having a body mass that operates at those scales would not be evolutionarily advantageous. Thus the structure of a complex adaptive system can be understood in large part as an interaction with pattern and process at discrete spatial and temporal scales.

The discontinuity hypothesis has been formally extended to other complex systems, such as cities and firms. Regional city size distributions and firm size distributions were found to be discontinuous, consisting of aggregations of similarly sized cities and firms, separated by gaps (Garmestani et al. 2005, 2006, 2008). The pattern of clusters and gaps for city sizes was conservative across 100 years of data. Although this is compelling evidence in favour of the theory of multi-scaled hierarchies of structure in complex systems, there is also a body of evidence demonstrating that city size, firm size, growth rates, and animal size distributions fit a power law distribution (Zipf 1949; Brown & Nicoletto 1991; Stanley et al. 1996, 2000; Canning et al. 1998; Axtell 2001; Marquet et al. 2005; Luttmer 2007; Batty 2008). Scale invariance is a hallmark of self-organized complexity (Kurakin 2009). However, evidence for scaling laws that represent a process that operates the same way across a wide range of scales and for which the mechanism is well understood is small. Many power laws describing economic and ecological variables often fail to be compelling for a variety of reasons. There is often a poor fit in the tails of the data (Stanley et al. 2000; Durlauf 2005; Luttmer 2007; Batty 2008; Gabaix 2009), and this suggests that different processes are at work in the tails. For example, one of the best known scaling laws is Zipf's law, which predicts that city size distributions will be continuous and fit a linear power law because growth rates are independent of size

and vary randomly (Zipf 1949; Gibrat 1957). Garmestani et al. (2008) showed that the power-law fit masks ranges of scale over which different power laws fit—in other words, the data is discontinuous, and power laws fit over a cluster of similarly-sized cities, as opposed to over the entire distribution (see also Cao et al., 2014).

Discontinuities not only fit the data better but are more relevant for understanding why some cities grow faster than others (Garmestani et al. 2007). Claims of a power law fit are often made for data that only represents a limited range of scales, whereas scale invariance presumes that processes are invariant across a wide range of scales (Avnir et al. 1998; Cristelli et al. 2012). There is often no link to a mechanism or even plausible reasons as to why a power law fit makes sense. Durlauf (2005) cogently makes this argument for many of the power laws found in socio-economic variables. It is likely that many of the power laws detected in economic and other data types are artefactual rather than reflecting a meaningful process, because power laws can be generated from purely stochastic processes, as well as dimensional relationships between variables (Avnir et al. 1998; LeBaron 2001; Lux 2001; Brown et al. 2002; Stumpf & Porter 2012) (though see Kurakin, 2009 for example of stochastically-generated power law behaviour with biologically sound mechanism). Finally, we suggest that too often the real point is missed in the power-law debate—if a power law or fractal dimension fits the data, then what does that tell us about the mechanism generating scale invariance, the impact on system structure and dynamics, and the policy implications? Does the power law hold over time, or is it a feature of a system in a critical state (Bak & Paczuski 1985)? Alternatively, what are the implications if data does not fit a power law? Avnir (1998) argues that even though many purported discoveries of fractals hold over such

a limited range of scales (on average about one order of magnitude) as to render their fractality questionable, researchers still derive benefits from framing the research in terms of a power law, because it “allows one to correlate in a simple way properties and performances of a system to its structure and to the dynamics of its formation”. This is precisely what we would argue for the method we present here: identifying the fundamental scales of structure in a system allows us to analyse the processes pertinent to their formation, and how emergent phenomena of interest can arise from that structure. In our experience, it is where data deviates from scaling laws that the interesting dynamics occur (Avnir et al. 1998; Bettencourt et al. 2007, 2010).

The question therefore becomes, are economies discontinuous with regards to their size, as represented by GDP? If economies fall into discontinuous size classes, and furthermore, if those size classes are robust over time, then it suggests that 1. the processes that structure GDP vary across spatial and temporal scales (i.e. are not scale invariant); and 2. the perspective offered by the discontinuity hypothesis on scaling in the global economy could drive novel insights into disparities between poor and wealthy countries.

Discontinuity analysis as methodological choice has benefits, including that the methods are not sensitive to either measurement error or missing data (Nash et al. 2014a), unlike the convergence literature where measurement error can have a significant impact on results (Durlauf et al. 2009). Nor are there issues of initial position, whereby the selection of the year used as the initial baseline for calculation of convergence can change results, all common issues in the convergence literature (Bloom et al. 2003; Canova 2004). Because we used a metric (GDP) available for all countries, data limitations do not constrain or bias pattern expression or restrict the

implications of our results. The method does not require averaging or aggregating data across years, an approach which risks losing interesting deviations as it can only represent average behaviour (Quah 1996b). Nor does data require binning, which can blur the number of aggregations that can be detected (as in Bianchi, 1997; Paap & Van Dijk, 1998). There is no need to manipulate the data extensively, as is common to many convergence analyses.

Furthermore, discontinuity analysis has no *a priori* subjective constraint on the number of possible groups or the membership within groups based on assumptions of shared initial conditions. There are no assumptions regarding the identity of the processes structuring the scale domains (analogous to clubs), so there is no risk that the choice of metric misses the mark entirely or is a stand-in for something else. Our approach makes no assumptions about the identity of the countries in each aggregation from year-to-year, so makes no assumptions about behaviour over time—it is concerned with whether or not there are aggregations and gaps in similar locations over time, which is indicative of scale domains independent of the identity of the countries within those aggregations. This means there are also no assumptions about mobility, as Pittau (2010) and others make. We make no assumptions about equilibrium or any other dynamics. Perhaps most importantly, our method is embedded within a well-developed theoretical framework. This theory includes multi-scaled hierarchical system architecture, multiple alternative regimes governed by different structuring processes, and thresholds that control movement between regimes, so provides a robust framework within which to discuss the results (Dakos et al. 2011; Lenton et al. 2012; Nash et al. 2014a; Allen et al. 2014).

Methods

We used real GDP (GDP in 2005 constant dollars) and country population data from the United Nations Statistics Division (United Nations Statistics Division 2012) to calculate a constant GDP per capita for all the countries of the world, for each year from 1970 to 2012; this was the maximum temporal extent of data availability for all countries. The number of countries changed as countries were formed or dissolved, so both the sample size and the identity of the countries from year-to-year is dynamic. All data were log-transformed, and each rank-ordered distribution was analysed for discontinuities using two methods, Monte-Carlo simulations using a uni-modal null (e.g., Restrepo et al., 1997), and Bayesian classification and regression trees (BCART) (Chipman et al. 1998), as is recommended (Stow et al. 2007). Our Monte Carlo approach compares the observed size distribution with a continuous unimodal null distribution generated by smoothing the observed data with a kernel density estimator (Silverman 1981). The null distribution is sampled 4000 times and the probability that the observed discontinuities in the size distribution occur by chance is calculated as a Gap Rarity Index (GRI) statistic and tested for significance. The BCART is a Bayesian implementation of a classification and regression tree which performs a stochastic search over the space of all possible trees, using prior probabilities of a split occurring at any given node. The log integrated likelihood is used to select the best tree. Previous experiments with the sensitivity of the BCART to selection of prior probability determined that the number of iterations was more important, so standard procedure is to use a fixed prior of 0.5 and run 1 million iterations, 25 times. The results of the Monte Carlo approach were confirmed with the BCART results.

Countries that bounded the distribution were permitted to be a group of one if they met the simulation significance threshold, while groups elsewhere in the data needed a minimum of two countries to be classed as a group.

Once we identified the groups and discontinuities, if present, we generated a dissimilarity matrix for the purpose of comparing the dissimilarity of the distributions using non-metric multidimensional scaling (nMDS), a non-parametric ordination technique (Clarke 1993). The nMDS uses only rank information and makes no assumptions about linearity or non-linearity (Zuur et al. 2007; Oksanen 2013). We were primarily concerned with capturing broad changes in distribution structure over time, so created the nMDS matrix to represent that group/gap structure. The rows of the matrix spanned the range of GDP values in the entire data set from smallest to largest, but were expanded to three decimals (GDP was rounded to two decimals) in order to account for the discontinuities, or gaps. Columns represented each year of data. The matrix cells were filled in with 1's and 0's, whereby a 1 indicated the presence of a country at that particular GDP value in that year, and a 0 represented an absence of a country for that particular GDP in that year. The entire aggregation from smallest to largest GDP was coded as a continuous 1, or presence, and the discontinuities between aggregations were coded as 0's, or absences. The nMDS uses this matrix to calculate all pairwise distances among samples, or each year of data. Once the number of dimensions was selected, the distance between each sample is plotted in ordination space, allowing for the visual assessment of the degree to which the distributions have similar structure from year to year. If the location of the discontinuities and the extent and location of each aggregation was completely

random, then this would be apparent in the distance and placement of each year's distribution to the others in ordination space.

The nMDS was conducted using metaMDS in package vegan in R 3.1.2 (R Development Core Team 2016). The dissimilarity matrix was created using Euclidean distance for binary data (Nash et al. 2014b). Multiple dimensions were plotted in a scree diagram to find the lowest dimensionality with an adequate ordination fit as expressed by a stress value (<0.2 , Clarke, 1993). A cluster analysis using function `agnes` from package `cluster` and `method = average` was performed to detect groupings of years with similar structure. The cluster dendrogram was arbitrarily pruned to show 6 clusters. This was considered a reasonable compromise between the two extremes of all years in 1 cluster, and all years in individual clusters. As the number of clusters increases from three, which consists of one outlier and two large groups, the two large clusters break into increasingly smaller sub-groupings without ever mixing in years from the other large cluster. There is no data to suggest how many clusters is 'best'. The nMDS was overlaid with the cluster results, in order to show groupings in ordination space.

An ANOSIM (Analysis Of Similarities) compared two timespans of the data. Group 1 encompassed 1970-1989, and Group 2 1991-2012. These groupings captured the substantial increase in countries that occurred between 1989 and 1991, mainly due to the dissolution of the USSR, in order to assess whether the change in n was partially responsible for the large distance that occurred between 1989 and 1991 in multivariate space. We removed 1990 for the ANOSIM, as it is not possible to have a group of 1 country in an ANOSIM, and the number of countries increased from 186 in 1989, to 197 in 1990, and to 208 in 1991. We ran 999 permutations. The

ANOSIM generates an R statistic and a significance value for that statistic and denotes the degree to which the difference between the two groups is higher than the within group differences. The axis scores from the nMDS were used in a spearman rank correlation analysis to see if the differences in structure between the distributions of countries in multivariate space explained movement along one or both of the axes in the nMDS. The structure of each distribution was assessed in the ANOSIM using 6 metrics: the total logGDP difference in wealth between the richest and poorest country; the number of countries; the number of aggregations; the average size of the gaps in logGDP; the average number of countries within each aggregation; and the average span of each aggregation in logGDP. These metrics described the basic discontinuous structure of each distribution.

Results

The number of countries ranges from 186 in 1970, to 210 in 2012. We found that in all years the distributions of per capita constant GDP are discontinuous, with groups of similarly sized economies separated by discontinuities, or gaps (Figure 1). Furthermore, many of the gaps are conservative and persist across the 43 years of data, particularly in the bottom and top thirds of the distributions. The middle of the distribution tends to be more variable, with gaps persisting in the same location for fewer than half of the years. The overall picture is one of conservative discontinuous structure, with some variability in the persistence and location of gaps between years, and more variability in the middle of the distributions. If the discontinuities are artifactual, then we expect more randomness and variability in the tails of the data, rather than the centers. However, even in the center of the distributions there are gaps that are present in 25-50% of the years.

In general, the total difference in wealth between the poorest and richest country narrowed over the span of the data. Similarly, the number of aggregations declined over time, as did the average size of the gap between aggregations. The average number of countries per aggregation increased, as did the average span of an aggregation (Figures 1-4 in Appendix A). The number of aggregations varied from 3 to 10, but more than 50% of the years had either 4, 5, or 6 aggregations (Table 1 in Appendix A).

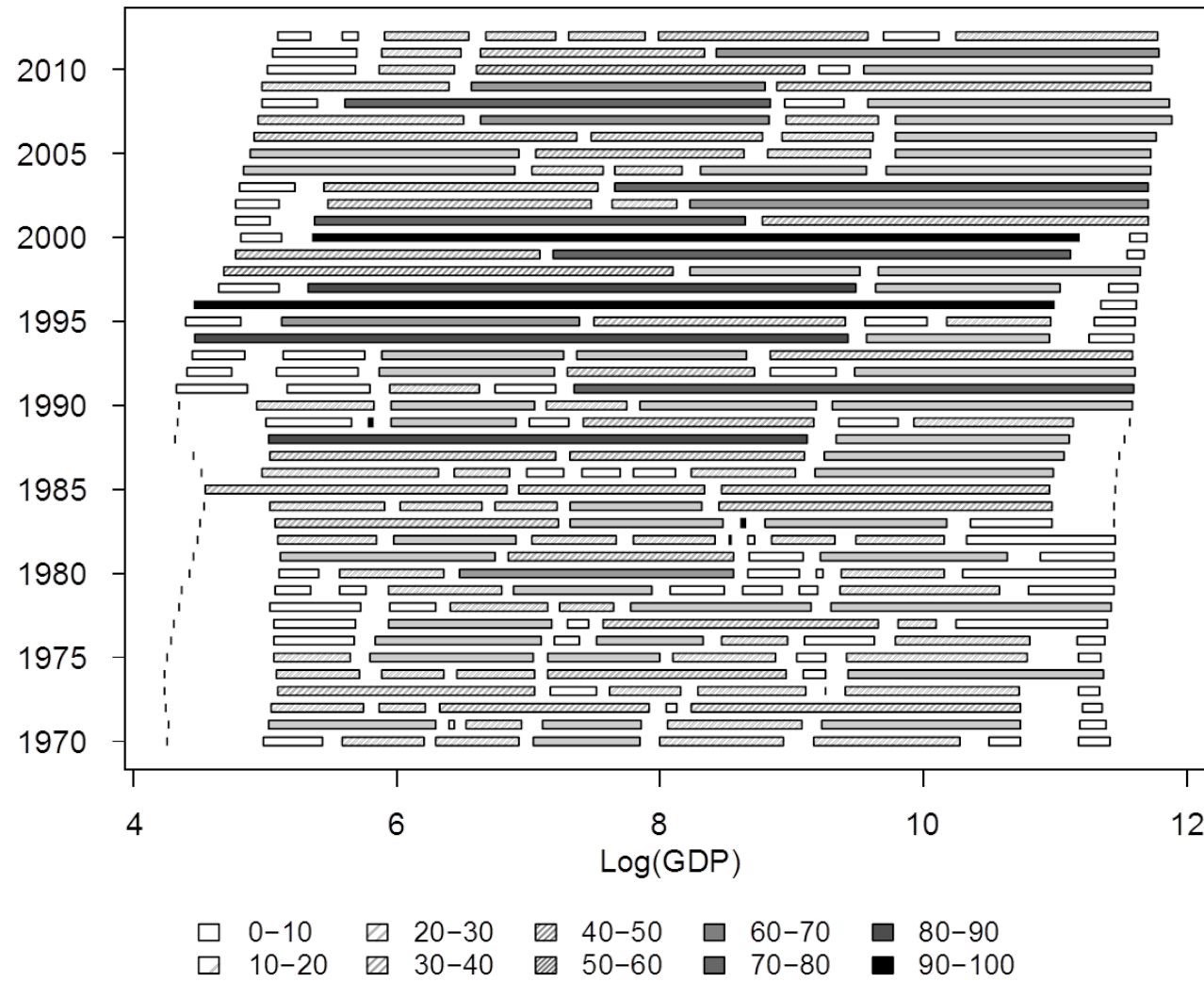


Figure 2.1 Yearly discontinuous distribution of constant (2005) per capita GDP for 43 years. Shading represents the proportion of countries falling in each cluster. ([Figure 2.1.pdf](#), 27kb)

The result of the nMDS on the per capita constant GDP show that in general, the distribution for each year is more similar in structure to the years that come before and after it than to years from which it is temporally separated, implying a conservativeness to the group/gap structure over time (Figure 2). However, the cluster analysis overlaid on the nMDS reveals that there are groupings of years that are more similar to each other than to other clusters (Figure 2). Interestingly, the two largest clusters capture broad movement along the y-axis, which correlates with unknown factors (see spearman rank correlation analysis below). Two dimensions were sufficient to capture the complexity of the data with an acceptable stress value (0.1937). The ANOSIM results, which compared two groupings of years (1970:1989 and 1991:2012) were significant ($R = 0.54$; $p < 0.001$), suggesting that the difference between the two groups is greater than the differences in multivariate structure within each group (Figure 3). This confirms our expectations that the abrupt change in the number of countries which occurred in 1990 and 1991 played a role in the large distance in ordination space between 1989 and 1991.

Figure 2.2 Ordination results for the two-dimensional non-metric multidimensional scaling (nMDS), showing the dissimilarity between years in terms of their structure of aggregations and gaps. The clusters represent years which are most similar to each other.

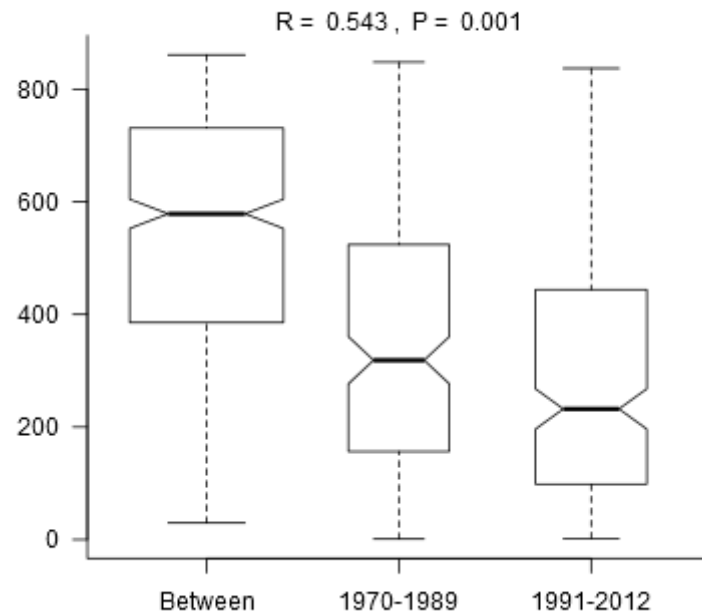


Figure 2.3 An ANOSIM (Analysis Of Similarities) between 1970-1989, and 1991-2012, to test whether the change in n between 1989 ($n = 186$) and 1991 ($n = 208$) was responsible for the large distance between these two years in the nMDS. Both the R and p -value indicate that the difference between the 2 groups is higher than the within-group differences.

The spearman rank correlation analysis, which evaluated the degree of correlation between the nMDS axis scores and the metrics capturing the structure of each distribution shows that the spread of the years along the x-axis (axis 1) is highly correlated with the structure of the distributions (Table 1), as all of the metrics are strongly correlated to the axis 1 scores. That is, the movement of years along axis 1 was explained by a decrease in the overall span of wealth (range in logGDP from poorest country to richest country), an increase in the number of countries, a decrease in the number of aggregations (Figure 4), a decrease in the average gap size, an increase in the number of countries per aggregation, and an increase in the average

logGDP span of an aggregation. The location of the distributions along the y-axis (axis 2) are not correlated to these structural metrics, with the exception of a moderate positive relationship with total span of wealth encompassed by the distribution (Spearman's $\rho = 0.38$, $p = 0.01$). This means that these metrics only partly explain the relationship of these distributions to each other in ordination space, as they are strongly correlated to only axis 1.

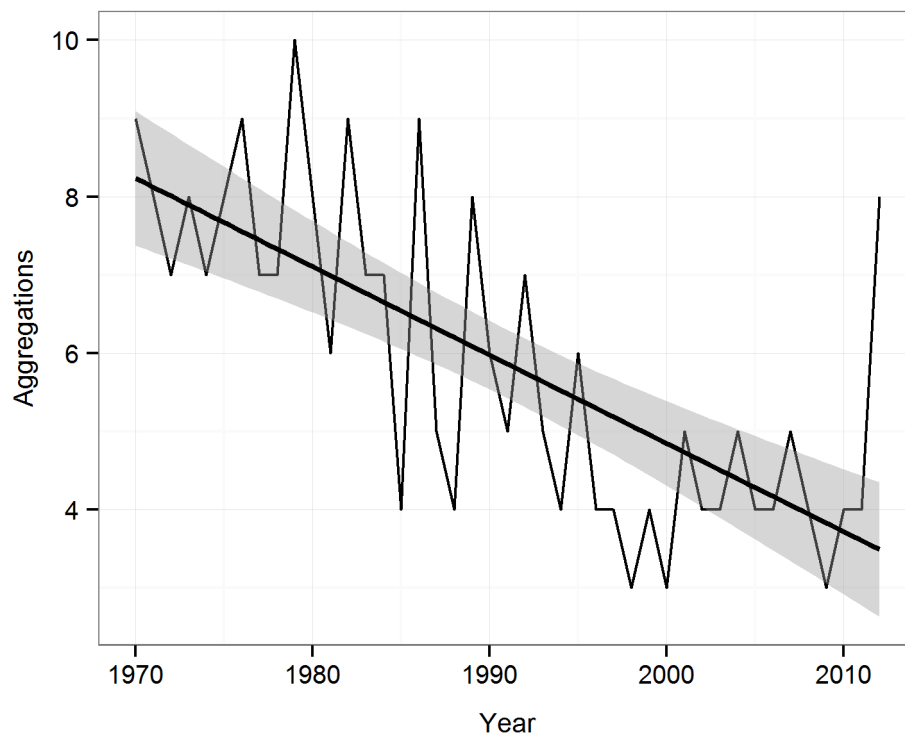


Figure 2.4 Change in number of aggregations over time.

Discussion

We analysed 43 years of GDP data representing all countries, and found that the rank-ordered size distribution for each year had a pattern of aggregations and gaps, where aggregations of similarly-sized economies were separated by discontinuities, or gaps in the distribution. These discontinuous distributions suggest that as with ecosystems, city sizes, and firm sizes, there are scale-specific structuring processes that create persistent scale domains (Garmestani et al. 2005; Allen & Holling 2008; Nash et al. 2014a), as the pattern of the aggregations and gaps is largely conservative over time. That economies fall into distinct size classes which are conservative over time has fundamental implications for understanding the processes that shape a country's GDP, and could help to resolve some of the inconsistencies in the convergence club literature. This analysis provides a foundational first step in understanding the multi-scaled structure of the global economic system, and the economies of which it is comprised, as a complex adaptive system.

The persistence of the pattern of aggregations and gaps was particularly strong in the lower and upper thirds of the distributions, and aligns with the most consistent results from the convergence club literature, namely, that the poorest and wealthiest nations belong to distinct convergence clubs (Quah 1996a; Bloom et al. 2003; Apergis et al. 2012). The muddying of the pattern of aggregations and gaps in the mid-ranges of the data is also supported by the convergence club literature, as analyses which allowed for more than two clubs found a strong pattern of poor and rich clubs, with transient clubs in the middle that have been proposed as regions that facilitate movement from the poor to wealthy end of the spectrum (Battisti & Parmeter 2013; El-Gamal & Ryu 2013).

The multivariate analysis highlighted that the persistence of pattern over the years was not random. The nMDS treats each year as a ‘community’, and measures the pairwise distance of each community in terms of dissimilarity in structure (location of aggregations and gaps on a continuum of logGDP). We represented structure via the pattern of aggregations and gaps, so the nMDS compares how similar the aggregation/gap structure is between years and then plots it in ordination space—in this case, in two dimensions. This visual representation reveals that as we move through the years the pattern of structure is largely retained, but also changes over time. So 1970 is furthest from 2012, but also distant from 1991-1993. If we traced a line through the years in chronological order, it would zigzag. This suggests that the number of aggregations and the location of gaps is patterned but not static, nor does it change smoothly from one year to the next. This is what we would expect in a highly dynamic state space governed by non-linear or rapidly changing processes. The spearman correlation analysis showed that the location of each distribution along axis 1 (the x-axis) is highly correlated to the structure of each distribution. However, movement along axis 2 was not related to the structural metrics, indicating that there are other factors driving the differences between distributions. Further work should test if axis 2 is correlated to econometrics such as those commonly assessed in the convergence club literature for their relationship to club formation; or to major disturbance events, such as wars or recessions.

Basins of attraction and resilience

Concomitant with the shift in the focus from convergence for all to convergence clubs for subgroups has been a shift in the neoclassical perspective that viewed economies as equilibrium systems, to one somewhat more in line with the

theory of complex systems, which posits economies as non-linear, non-equilibrium systems that reside within basins of attraction. If indeed economies operate in a state space such that system variables will dynamically move towards a system attractor, then there are repercussions of such dynamics and behaviour that impinge on many other assumptions with regard to the short- and long-term structure, behaviour, and dynamics of economies, and these have not been effectively dealt with in the economics literature.

Similar to the convergence literature, our approach cannot analytically demonstrate that the scale domains identified are actual basins of attraction. We can, however, frame our findings in the context of complex systems theory and basins of attraction, ensure that we do not violate the assumptions of that theory in doing so, and evaluate whether our results are consistent with theory. Our analyses support a conceptualization of economies as complex adaptive systems, operating within a global economic state space. Basins of attraction are the regions within a state space for which a set of initial conditions will converge towards the same attractor. A state space can have more than one basin of attraction, and both the state space and the basins are dynamic over time and space (Mumby et al. 2014; Bozec & Mumby 2015). Basins can change shape as a result of endogenous and exogenous forcing, and they can be temporally transient, as the state space can be altered to either allow or disallow the development of new attractors (Scheffer 2009a).

If the set of national economies are the entities operating in the global economic state space, then our results suggest that there are some deep basins of attraction operating in the upper and lower portions of the country distribution, while

the middle ranges of the distribution may be a more dynamic region with shallower basins potentially winking in and out of existence (Figure 5).



Figure 2.5 The ball and cup heuristic represents a simplified state space with multiple basins of attraction. The x-axis is the discontinuous distribution of GDP. Each valley is a basin of attraction, analogous to an aggregation of similarly-sized countries, as identified in the discontinuity analysis. The threshold which must be surmounted for a country (represented by the ball) to move into a wealthier basin tends to increase along the x-axis. The lower and upper thirds of the distribution have larger and deeper basins, while the central basins are shallow, close together, and easier to move between.

Implications of aggregation/gap structure for economics

The finding of discontinuous structure in economies suggests that economists can utilize the extensive literature pioneered in other fields to explain dynamics in complex economic systems. Identifying discontinuous structure is only the first step; one cannot infer from the discontinuous structure what creates it, but detecting said structure without any observer bias is an important first step for objectively identifying patterns of complex systems. This provides the basis for the next step, which would be to identify the key processes responsible for structuring the scale domains, and determine the extent to which they are coincident with the processes

already found to be critical in the economics literature (e.g. Alfonso-Gil et al., 2014). Doing so in the context of the discontinuous structure identified explicitly incorporates scaling into analyses, and may help resolve the often inconsistent results found in the economics literature, where a process highly relevant to one convergence club or one analysis is less so in another. Although there are processes such as competition and market niche exploitation which are scale-invariant, we would expect that many processes operate over a limited range of scales, or operate differently at different scale domains.

There are similarities but also clear differences between economies and ecosystems (Garmestani et al. 2009a, 2009b). The processes known to be critical in economies are typically human in origin (such as governance, technological development, or investment in education), whereas many of the key processes in ecosystems are biotic or abiotic in origin and often less directly controlled by humans (such as precipitation, fire, and herbivory). Although both are open systems, ecosystems tend to be more loosely coupled to each other than economies, which have more direct, strong, and dynamic relationships and feedbacks between each other. Whereas species evolve body sizes in an evolutionary theatre that is only slowly changing in the dimensionality of ecological structure, economies are comprised of slowly-changing people embedded in relatively fast changing societies. The extent to which human agency introduces dynamism in the state space of economies is unknown, but we recognize that there is likely to be more variability than we see in the scale domains present within and across ecosystems (though see Barabasi, 2010). That said, our results suggest that there are, nonetheless, fundamental scaling processes in the economic state space that are sufficiently persistent to create discrete

scale domains of economic opportunity, particularly in the upper and lower ranges of the distribution. The key processes structuring these scale domains may well be the same processes already widely analysed by economists for their role in wealth creation, more recent advances such as metrics of diversity in product space (Hidalgo et al. 2007; Hidalgo & Hausmann 2009; Hausmann & Hidalgo 2017), or may be more fundamental to the biology of humankind, such as competition, neurological hard-wiring that structures population sizes (Kosse 1990; Dunbar 2008), the tension between self-interest and the ‘we’ (Lynne 2006), or the tension between diversity/redundancy that appears to characterize all complex adaptive systems (Zipf 1949; Lee et al. 1998; Page 2010a). More generally, our results suggest that economies adhere to similar structuring processes observed for a series of complex systems, including ecological and social (Allen et al. 2014).

Testing these hypotheses in economic systems could focus on whether the aggregations of economies identified by the discontinuity analysis are correlated with economic processes, just as the convergence literature has analysed the relationship between processes/economic metrics and club formation. A fundamental difference is that the aggregations detected are not subjective groupings constrained in the number of groups that can be detected, assumptions of shared initial conditions, or binning or other data manipulations (as in Paap and Van Dijk, 1998). The pattern present in the aggregation/gap structure is more likely to reflect underlying processes and patterns representing scaling forces in the global economy than patterns derived from arbitrarily selecting levels of observation and equating them with fundamental scaling processes. Another possibility is to focus on the movement of countries into and out of aggregations. While Pittau and Zelli (2010) and Galor (2010a) and others assume

that immobility is a defining feature of convergence clubs and of basins of attraction, it may be that the basins of attraction for the poorest and wealthiest countries are particularly deep, with a high threshold which must be surmounted to depart the basin. Our evidence supports this speculation, as the pattern of aggregations and gaps in the tails of the data are the most similar over time, and this would also account for the relative immobility of countries within those basins (Canova 2004; Battisti & Parmeter 2013). The variability of the mid-ranges suggests shallower and more transient basins of attraction, where the processes structuring them are more dynamic over the years.

Whether the discontinuous distribution of economies represents a series of basins of attraction remains an outstanding question, and perhaps dependent on our choice of GDP metric. We also performed a discontinuities analysis on constant GDP without adjusting for population size, and the pattern of aggregations and gaps was similar to that of per capita GDP, but the gaps were more consistently present over time (Supplement Figure 6). Economies are constrained in their size by factors such as geography and the material resources present within the system, as well as history and the events which have played a role in their structuring. Adjusting for population size accounts for some of these inherent differences between countries, which may be why the aggregation and gap structure was clearer in the real GDP data than in the real per capita data. Using real GDP may also conflate two things (size of population and size of economy) which interact, but are structured by different process. Regardless, using real GDP masks critical qualitative differences between economies in the same size aggregation, as some of the countries may be in a poverty trap, whereas others may be quite wealthy for their size. Having both kinds of countries in

the same basin of attraction is not sensible, as they are clearly being structured by different processes. Adjusting for population size accounts for this difference, making it more likely that the aggregations reflect countries in the same basin of attraction.

Reduction in number of aggregations

We interpret the decrease over time in the number of aggregations as a loss of a particular kind of complexity. There was a steady reduction in the number of aggregations over the years, with a sharp reduction beginning in 1996 and persisting through 2011. This suggests that there are fewer scale domains and fewer key processes structuring the size of economies. These findings are consistent with graphs in Pittau et al. (2010), which show a reduction in the number of modes over similar timeframes using a kernel density approach, and other convergence work showing increasing distance between the wealthy and the poor (Quah 1996a; Pittau et al. 2010). A simplification of cross-scale structure, as manifested in a reduction of scale domains, is a loss of levels in the hierarchy of the global economy. In short, there are fewer basins of attraction. This has no normative connotation, but the non-random trend over time speaks to a simplification in the number of key processes that structure economies. This is relevant because over time, CAS's tend to grow in their complexity in order to capture and dissipate more energy and retain more material within the system (Schneider & Kay 1994; Beinhocker 2006; Hidalgo & Hausmann 2009). The complexity of a system derives from a multiplicity of features, including the heterogeneity of its parts, the number of them, the degree of connectivity between them, and the diversity and number of hierarchical levels, among others. For example, had we data from previous centuries, we would expect to see an increasing

number of aggregations over time as economies and the world have increased in complexity across all these features (Schneider & Kay 1994; Ulanowicz & Abarca-Arenas 1997; Beinhocker 2006). A reduction in the number of aggregations suggests a particular kind of simplification, in which fewer processes are responsible for generating scale domains (basins of attraction). This is not contradictory to the ongoing increase in economic complexity with regards to the increase in output diversity and complexity in production (Klimek et al. 2012). The reduction we observed may reflect the following, which are not mutually exclusive: a) a world with increasing connectedness between national economies and therefore a reduction in the number of key processes structuring the relative wealth of countries; b) a partial collapse of complexity, where resilience to disturbance is reduced and the ability of economies to capture and dissipate energy is diminished (Schneider & Kay 1994; Hidalgo & Hausmann 2009); c) the network of economies is over-connected, rendering the global network vulnerable to cascading disturbances (Gunderson & Holling 2002; Pascual & Dunne 2005; Havlin et al. 2012); d) a reduction in resilience, as quantified by the contraction in the number of scale domains and thus a loss of heterogeneity. These possibilities were demonstrated in the 2008 recession, but the sharp reduction in the number of aggregations occurred well before that in 1996, perhaps suggesting a reduction in the resilience of the global economy prior to the onset of the recession.

Conclusion

The relevance of both our work and that of convergence clubs lies in uncovering groupings of countries that may represent fundamental structuring processes in economic systems. The difference between the two approaches is that

our method does not violate assumptions of complex systems theory, can objectively identify system scales, and makes few assumptions about the data. The robust pattern of discontinuities in cross-national GDP over 40+ years strongly supports assumptions of complex adaptive systems theory regarding scaling and non-linearities in pattern and process, and warrant further explorations with regard to specific processes which may structure the identified scale domains. An understanding of the key processes governing each scale domain might improve our ability to manage those processes to achieve two fundamentally distinct things: facilitate the movement of an economy from a smaller scale domain to a larger by moving the economy towards the threshold defining the basin of attraction so as to facilitate a shift to another scale domain (synonymous with basin of attraction); or work to maintain the resilience (shape of the basin of attraction) of a desirable basin so as to more readily stay within a particular GDP aggregation. Both ecology and economics have much to offer on these goals. There is a burgeoning literature in ecology on basins of attraction, regime shifts, and thresholds, while economics has much to offer on understanding the processes that drive growth and wealth creation.

The movement away from linear equilibrium models in economics is marked, but has not manifested in a rigorous uptake of complex systems theory. In many cases, neoclassical ideas of global convergence have merely been expanded to include multiple such equilibriums without altering fundamental assumptions about long-term dynamics and behaviour. When an attempt to incorporate pieces of alternative theories has occurred, few researchers incorporate all of these changed assumptions and dynamics into their models at the same time, nor have they defined their new terms and assumptions in a robust manner. If the base model is still equilibrium in

nature, than only one or two assumptions can be relaxed at a time (Beinhocker 2006), and even if the model is not predicated on equilibrium, it can be challenging to incorporate all the assumptions of complex systems dynamics due to methodological or data limitations. The implications of a bimodal world bifurcated between rich and poor is a simpler and more tractable model than that of a multi-modal, multi-scalar world with different processes driving the creation and maintenance of each mode or basin. As Ricardo Hausman (2012) wrote, “In trying to understand the nature of economic reality we have been much less willing to let the world tell us what it is made of and more willing to believe our theoretical contraptions”.

CHAPTER 3 PROCESSES THAT STRUCTURE SIZE CLASSES IN GDP

Introduction: From ecosystems to economies

Ecosystems are physically structured by processes that occur at spatial and temporal scales that are often separated by magnitudes of order. Theory suggests that there are only a small number of processes that generate a size class, and they are not the same across all scales of a system. Photosynthesis occurs at small and rapid spatial and temporal scales, while geomorphological processes drive the location of biomes over thousands of kilometres and century to millennial timescales. The relationship of these scaled processes to species occurs through the medium of the physical structure of ecosystems; where and when resources occur in time and space. Animal body masses are strongly discontinuous in ways that correlate to the scales of physical structure available to them as resources (Nash et al. 2013b). A mouse can forage on the seeds of a singular plant that would not even be perceived as a resource opportunity by a much larger animal. This relationship is also bi-directional, in that both plant and animal species modify their surroundings and physical structure to promote the persistence of the resource structure on which they depend (i.e., there are strong positive feedbacks)(Kareiva & Bertness 1997).

The extent to which this process-structure-species construct applies to economies is uncertain, but the fundamental architecture of complex adaptive systems, including economies, is multi-scaled and hierarchical as a result of self-organizing processes that convert as much information, or thermodynamic energy, as

possible (Schneider & Kay 1994; Beinhocker 2006), and this suggests that economies will be impacted by similar process-structure organizing principles. Furthermore, previous research (see Chapter 2) has demonstrated that economies fall into distinct size classes indicative of scale-specific processes creating basins of attraction. However, whether economic processes occur at distinct spatial and temporal scales sufficient to create scaled basins of attraction that represent economic opportunity at that range of scales is an open question. Individual economies are clearly multi-scaled and hierarchical with many levels of organization, but the processes that would potentially structure a network of economies are less obvious. Are smaller economies structured by processes that occur at smaller and more rapid spatial and temporal scales than larger economies, or, as in work on city sizes, is growth rate variable among different scales/size classes (Garmestani et al. 2007)? Conversely, it may be more appropriate to think of economies as a spectrum of poverty to wealth processes, where scaling is disconnected from space and time, and economies are instead a function of scale-invariant or scale-neutral processes that structure relative wealth, as expressed by per capita Gross Domestic Product (GDP).

It is well established that individual countries are not on identical growth trajectories, and do not share a common path to wealth (Durlauf & Johnson 1995; Quah 1996a; Phillips & Sul 2009; Apergis et al. 2012). Regardless of the economic metric evaluated investigations have found a minimum of two groupings of countries, the rich and the poor, where countries within a group either share a similar rate or are converging towards a similar rate for the metric under evaluation. When methodologies allow for it, researchers have found more than two groupings (Durlauf & Johnson 1995; Apergis et al. 2012; Battisti & Parmeter 2013; El-Gamal & Ryu

2013), implying that multiple processes may differentially govern wealth and generate groupings of countries that are more complex than suggested by simple division into rich and poor countries.

These groupings are generally referred to in the literature as convergence clubs (Baumol 1986), and are part of a body of work motivated to understand disparities in wealth between rich and poor countries. For the most part, this literature does not stray far from the assumptions of neoclassical economics, which assumes a single linear equilibrium state for all cross-national economies, and seeks to understand how and why countries deviate from this equilibrium. More recently, there has been a push to consider alternative assumptions for economic behavior, which include the possibility of multiple stable states, or multiple groupings of countries with shared econometric(s). These studies explicitly allow for the possibility of multiple convergence clubs, and they consistently find them (Durlauf & Johnson 1995; Apergis et al. 2012; Battisti & Parmeter 2013; El-Gamal & Ryu 2013).

The discovery of multiple clubs, also conceptualized as basins of attraction, necessarily drives inquiry into the processes that structure the basins. Barro and McCleary (2003) wrote, “Previous research has used the experience of a broad panel of countries to assess the determinants of economic growth. One general conclusion is that successful explanations have to go beyond narrow measures of economic variables to encompass political and social forces”. A variety of studies have assessed social, cultural, political and financial metrics for their correlation with club membership, growth rate and wealth, with frequently conflicting results. For example, Yang (2008) found that democracy reduced growth volatility in countries with a high degree of ethnic heterogeneity, but had little effect in countries with a low

degree of heterogeneity. Tavares and Wacziarg (2001) concluded that democracy had both positive and negative effects of growth, similarly to Narayan et al. (2011) who found mixed results when exploring economic growth and political freedom, whereas Rock (2009) found that democracy caused growth and investment to rise in Asia. Alfonso-Gil et al. (2014) found that for the period 1850-2010, civil liberties and economic growth rate were positively correlated. Differences between methodologies, objectives, and the countries under investigation have made it difficult to arrive at broad generalizations regarding the relationship between the various cultural and financial metrics and convergence clubs. This has been exacerbated by differences in the assumptions of the various methodologies used to find clubs, as some methods *a priori* constrain the number of possible clubs, while others operate from differing assumptions regarding the realistic nature of a global growth rate and a single equilibrium point.

Similarly to the convergence club research, we evaluated cross-national per capita GDP, using a method from ecology that objectively identifies discontinuities in rank-ordered data, and identified persistent discontinuities and multiple size classes (i.e., convergence clubs) in 43 years of cross-national per capita GDP (Chapter 2). The method identifies gaps in the distribution that are larger than expected by chance, and thus breaks the distribution into groupings of similarly-sized countries based on their per capita GDP. The generic method can be used to identify discontinuities in any rank-ordered data. Canova (2004) argues that clustering is more prevalent than convergence, even within groups, as there is a significant dispersion of steady states around each basin of attraction, making perfect convergence rare. Discontinuity analysis presumes that survival at the boundaries of a basin of attraction is difficult,

resulting in gaps in a distribution, whereas convergence assumes an attractor which draws in trajectories. The two are not mutually exclusive, but assessing gaps makes fewer assumptions as a weak attractor may yield a wide dispersion in trajectories within a basin Canova (2004). More importantly, discontinuity analysis avoids pitfalls common to the convergence club literature (see Chapter 2). Too often, methods to identify convergence clubs in economies constrain or *a priori* select the number of possible clubs, or constrain the groupings to countries with a shared initial condition in an assumption that shared initial conditions is required to end up on the same attractor. Discontinuity analysis does not require the *a priori* selection of the number of possible clubs, makes no assumptions about shared initial conditions or the processes that might generate groupings of countries, and uses a metric available for all countries, thus is less vulnerable to methodological assumptions changing the patterns observed.

The groupings identified by a discontinuity analysis are, however, analogous to those identified by the convergence club literature. The convergence club literature tends to refer to the groupings as multiple stable states, or multiple equilibria, and occasionally as basins of attraction, though generally the attractor is presumed to be a fixed point equilibrium attractor. The term ‘stable state’ implies a rigidity that is inappropriate for complex systems such as economies or ecosystems, and using that term requires the caveat that stability can include high levels of natural variation and stochasticity, so it is only the state at the system-level that stays in a persistent recognizable configuration. As per Scheffer (2009b), we prefer the terms attractor and regimes, because they do not infer a stability that is unrealistic for complex adaptive systems such as economies. Our working assumption is that groupings

identified by a discontinuity analysis consist of countries operating in the same basin of attraction, with a regime defined by the key processes that structure the basin. Regimes imply that the system stays in a recognizable ‘state’, without inferring stationarity or a lack of variability within the system. Some economic researchers have claimed that movement between basins of attraction is evidence that the basins do not actually exist, as if stationarity within a basin is a definitional prerequisite (Galor 2010b; Pittau et al. 2010). We argue that movement between basins of attraction is not only possible, but highly probable if changes in key variables within a system or in the state space itself move a system close to a bifurcation, where even small parameter changes can cause the system to cross a threshold and move to an alternative attractor. Backwards movement along this trajectory to the previous attractor can be difficult and sometimes impossible due to hysteresis, if the bifurcation is what is known as a catastrophic bifurcation. To that end, identifying attractors in economic systems, as well as the key processes responsible for structuring a regime within an attractor is of interest, because it should facilitate an improved understanding of the key leverage points with which to either move a system (country) out of an undesirable basin, or maintain a system within a desirable basin.

Purpose

Our purpose is to test whether basic socio-cultural-historical differences among countries could be responsible for structuring discontinuous size classes in cross-national GDP. The novelty of our analysis lies in the assumptions of our research question and the objectivity of our method for testing for groupings. Our research question is grounded in assumptions regarding system behavior and dynamics derived directly from complex systems theory and ecological theory

regarding scaling processes in complex adaptive systems, and presumes that there is structure and hierarchy in the global economy, as well as non-linearity and non-equilibrium processes. Equally important, our methods make no data assumptions beyond the very general assumption that per capita GDP reflects something fundamental about the structure of global economies, and that size classes in wealth are non-random.

We focus our analysis on variables reflecting basic socio-cultural-historical differences among countries, but we recognize that these variables are often correlated to each other, and we also recognize that financial metrics such as aggregate factors of production, technology, or Hidalgo and Hausman's product space network complexity (2007; 2009) are also likely potential structuring processes in discontinuous cross-national economic distributions. We focus on socio-cultural metrics in part because they have received less attention in the economic literature as noted by Barro and McCleary (2003), but also because we are interested in whether the processes that structure economies are embedded in socio-cultural-political differences, are extant or neutral to those cultural differences, or are some combination thereof. Tantalizing studies on size classes in human populations suggest that there are 'panhuman' thresholds that structure population size classes, based on basic human hard-wiring that regulates individual information-processing limitations (Kosse 1990, 2001; Dunbar 2008). Some economic processes may be similarly scale-invariant, and operate in the same way across all economies regardless of size or socio-cultural-historical-political-geographic differences because they are inherent to being human. However, scale-invariant processes with realistic mechanisms are relatively rare in complex systems (Avnir et al. 1998; Durlauf 2005). What is more common are

processes that operate over a limited range of spatial and temporal scales, or have a different relationship at different scales, and generate discontinuities in the entities interacting with those processes.

Our hypothesis is that socio-cultural variables may play a role in structuring basins of attraction of countries with similar GDP, and we test whether social-cultural variables appear to strongly delineate size classes. Our choice of variables, therefore, is focused on socio-cultural variables for which the economics literature provides the strongest support for playing a role in economic growth, and for which there was sufficient data availability. We selected four variables: democracy, or degree of political and civil liberty, life expectancy at birth, religion, and colonial status. Previous research suggests that these are correlated with economic growth and/or relative wealth. Democracy appears to have a complex relationship with economic growth, as discussed earlier. However, it is not the fact of the relationship that is contentious, but the nature of the relationship—does democracy drive growth, or does growth increase democracy (Alfonso-Gil et al. 2014)? Investments in human capital, which include education and health care, as reflected in life expectancy, are similarly complex—does a longer life expectancy enhance economic growth, and/or does economic growth stimulate investments in health (Acemoglu & Johnson 2006; Berthélemy 2011; Cervellati & Sunde 2011; Barro 2013; Bloom et al. 2014)? As with democracy, the relationships between the components of human capital and growth appear to be non-linear and relative to current wealth. Religion is thought to influence economic outcomes because it is associated with personal traits of honesty and work ethics (Weber 2002); Barro and McCleary (2003) found that economic growth is positively correlated with a belief in heaven and hell. Finally, colonialism

is a driver of path dependency, in that a country's economic development over time may be a function of significant historical events, such as whether or not a country was ever a colony. Such a historical legacy may be significant enough to fundamentally alter a country's trajectory over time, and thus be a key driver in structuring the size of the economy. Much of the work on this issue has assessed different colonization policies or tenures, while we are more interested in the binary question of whether or not a country was a colony (Grier 1999; Acemoglu et al. 2001; Nunn 2009; Easterly & Levine 2012).

We begin with the simple premise that the distributions of GDP will be discontinuous, and that these four variables may have a role in structuring the distributions. The processes that structure ecosystems tend to occur at limited ranges of spatial and temporal scales and generate highly robust discontinuities in both ecological structure and the species that interact with both that structure and those processes; in other words, these key structuring processes create basins of attraction within the scale ranges over which they operate (Allen & Holling 2008; Nash et al. 2013b, 2014a). It is difficult to know *a priori* whether processes that structure economies follow a similar pattern or not. A variable such as life expectancy could structure economies of all sizes (across all scales) and have the same relationship at all scales, in which case we would expect that no gaps in the distribution align across each level of the variable because there would be no basins of attraction (i.e. gaps would not occur in the same location along the GDP axis for the 'High', 'Medium', and 'Low' datasets, or might not occur at all—gaps may still be present because processes unaccounted for in this analysis could be structuring size classes in GDP). Alternatively, life expectancy could structure economies across all scales but have a

different relationship at different scales, in which case we would expect to see gaps align across the levels of the variable (i.e. gaps would occur in the same location along the entire GDP axis for the ‘High’, ‘Medium’, and ‘Low’ datasets for life expectancy. Or finally, a variable may structure GDP but only at one or a few scales, in which case we would expect to see gaps occur in the same location at a limited range of scales across the datasets belonging to the same variable. If gaps are congruent in the latter two cases, we cannot claim a mechanistic relationship between the variable and the lump/gap structure, but neither can we exclude the variable as a possible driver. For example, life expectancy may play a critical role in structuring poor countries, but not wealthier. This scenario of variables affecting one or a few size classes would in total give rise to a globally discontinuous distribution. Finally, if the variables have no direct role in structuring size classes in economies, then we would expect no gaps to occur at similar locations across the levels of a variable.

We also performed a reverse analysis that asked whether an unsupervised multivariate method could group the countries into groups similar to those identified by the discontinuity analysis, given only each country’s classifications for the socio-cultural variables. We first ran a discontinuity analysis on the full complement of 190 countries to identify the lump/gap structure of the distribution using rank-ordered log GDP. Then we used Multiple Correspondence Analysis (MCA), a dimension-reduction technique that uses as input only each country’s classifications for the four socio-cultural variables. The MCA is not provided either GDP or group membership (groups having been identified in the discontinuity analysis). The question here is whether or not, given only the socio-cultural variables, the MCA could ‘correctly’ place each country on an ordination graph such that they were proximate to other

countries in the same size class grouping identified in the discontinuity analysis. If the MCA could successfully group countries, then the implication is that these socio-cultural variables explain the clusters of countries with a similar GDP value. In other words, membership in a wealth size class can be explained or partially explained by these 4 socio-cultural variables.

Methods

We used real per capita GDP (constant 2005 dollars) for 190 countries from 2010. Countries were classified by their status for each of the 4 socio-cultural variables previously shown to be correlated with membership in convergence clubs, and then for each variable were divided into sub-groupings based on having the same status for that variable. The variables are life expectancy at birth (3 levels), religion (3 levels), democratic status (3 levels), and colonial status (2 levels), for a total of 11 different data sets. We conducted a discontinuity analysis on each of the 11 data sets. Although other socio-cultural variables are also correlated with convergence club membership, there was insufficient country coverage; a minimum sample size is needed to run a discontinuity analysis ($n \geq 30$ recommended). Life expectancy data were from the United Nations (United Nations Statistics Division 2012), and we used the United Nations classifications of High, Medium, or Low life expectancy. Religion data were from the CIA World Factbook (Central Intelligence Agency 2010), which provides a percentage breakdown of the religions the population identifies with. We used the percentages to classify countries into 1 of 3 categories; countries were considered Christian or Muslim if $\geq 60\%$ of the population was so, or Other if $< 60\%$ of the population identified with one dominant religion. Democracy data came from Freedom House 'Freedom in the World' reports (2010) because they

provided the ‘thickest’ definition of democracy (included political rights and civil liberties) (Landman 2007), and covered the most countries. We used the Freedom House classifications of ‘Free’, ‘Partially Free’, or ‘Not Free’. Colonial status was binary (Yes or No) and came from Acemoglu et al. (2001).

GDP and country population data was from the United Nations Statistics Division (United Nations Statistics Division 2012) to calculate a per capita constant GDP for each of the 190 countries, which was log-transformed. The 190 countries were then broken into eleven separate datasets according to the socio-cultural variables. Specifically, the 190 countries were broken into 3 life expectancy groups ($n = 79$ ‘High’, $n = 49$ ‘Medium’, and $n = 62$ ‘Low’); 3 religious groups ($n = 104$ ‘Christian’, $n = 45$ ‘Other’, and $n = 41$ ‘Muslim’); 3 democracy groups ($n = 85$ ‘Free’, $n = 59$ ‘Partially Free’, and $n = 46$ ‘Not Free’); and 2 colonialism groups ($n = 128$ ‘Yes’, $n = 62$ ‘No’). Each of the eleven datasets was then individually analysed for discontinuities.

Two methods were used to detect discontinuities, as is recommended (Stow et al. 2007); a Monte-Carlo simulation using a unimodal null (e.g., Restrepo et al., 1997), and Bayesian classification and regression tree (BCART) (Chipman et al. 1998). The Monte Carlo approach compares the observed size distribution with a continuous unimodal null distribution generated by smoothing the observed data with a kernel density estimator (Silverman 1981). The null distribution is sampled 4000 times and the probability that the observed discontinuities in the size distribution occur by chance is calculated as a GRI statistic and tested for significance. The BCART is a Bayesian implementation of a classification and regression tree which performs a stochastic search over the space of all possible trees, using prior

probabilities of a split occurring at any given node. The log integrated likelihood is used to select the best tree. Previous experiments with the sensitivity of the BCART to the selection of prior probability determined that the number of iterations was more important, so standard procedure is to use a fixed prior of 0.5 and run 1 million iterations, 25 times. The results of the Monte Carlo approach were confirmed with the BCART results. A country was allowed to be a solo ‘group’ if it was at either extreme of the data, but otherwise a minimum of 3 countries was required to be a group. The eleven datasets were graphed on the same scale, so that the lump/gap distributions could be compared and assessed for congruence in the location of the lumps and gaps.

The Multiple Correspondence Analysis (MCA) was done in R v. 3.3.0 (R Development Core Team 2016) using package FactoMineR. MCA is an unsupervised dimension-reduction multivariate technique akin to Principle Correspondence Analysis that uses qualitative rather than quantitative data. Ellipses were calculated using the default type in `stat_ellipse` in `ggplot2`. Group membership was identified by using the discontinuity analysis on the entire complement of 190 countries.

Results

All eleven datasets had discontinuous distributions, which consisted of groups (lumps, or clusters) of countries with similar GDP, separated by gaps where there were no countries present for that range of GDP (Figure 1). The number of groups varied from 5 to 11 across the eleven datasets, with an average of 8.5 groups. A visual assessment of the distributions along the GDP axis (x-axis) shows some clear patterns in the data having to do with the correlation between these variables and wealth (Figure 1). For example, former colonies fall in the middle of the GDP

spectrum with the exception of the Democratic Republic of Congo, which is in a solo group and is the poorest country of all 190 countries. Conversely, not-colonies span the full range of GDP. Similarly, Christian countries span the entire GDP range, while Muslim countries and countries that are Other (a non-Christian/Muslim-dominated country) do not have countries in the tails of the data. Countries that are Free and have a High life expectancy fall on the wealthy end of the GDP spectrum, whereas countries that are Not Free and have a Low life expectancy fall on the poor end of the GDP spectrum, and countries with a Medium life expectancy are constrained to the mid-ranges of the GDP spectrum. Of the 4 variables, Life Expectancy is the most stratified by wealth. Many of the distributions do not span the entire breadth of possible GDP, so the extreme tails of the data cannot be meaningfully evaluated for congruence in gaps.

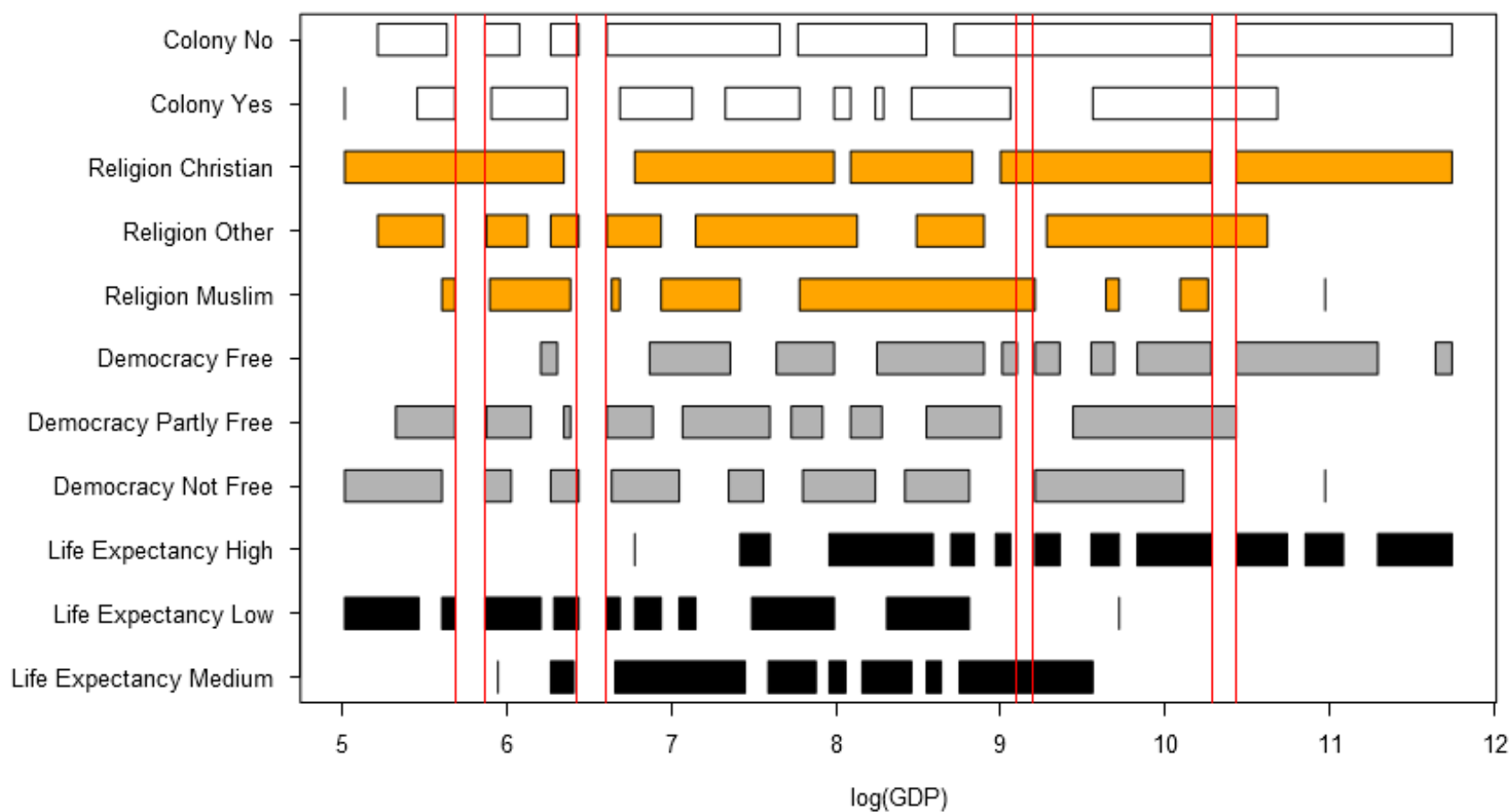


Figure 3.1 Discontinuous structure of the distributions partitioned by cultural variables. Vertical red lines represent gaps that occur across all or almost all of the distributions. ([Figure 3.1.pdf](#), 6KB)

When assessing the distributions specific to each variable, it is clear that the gaps rarely align across all the levels for each variable. In fact, in almost all instances where gaps align across two or more levels of a variable, they are also congruent across all levels of all variables; these master gaps are marked with red vertical lines (Figure 1). Neither colonial status nor religion have any congruent gaps beyond the master gaps, while democracy has 6 gaps that are congruent for 2 of the 3 levels. For life expectancy, the chance for congruent gaps is constrained by the fact that the distributions only overlap for a limited range of GDP, from 6.75 to 9.7 GDP. There are several places where 2 levels have gaps in the same location beyond the master gaps (log X GDP and log Y GDP, but never for all 3 levels. It is telling that there as many gaps that span all the distributions as there is congruence in gaps between levels of the same variable. The master gaps that span the eleven distributions appear to originate from structure in the complete data set. In other words, when we run a discontinuity analysis on the complete data set of all 190 countries, it identifies 5 groups and 4 gaps (Figure 2), and the location of the gaps along the GDP axis matches the gaps marked with vertical red lines.

Multiple Correspondence Analysis analyses systematic patterns of variation in categorical data and displays the results graphically in ordination space. Both the individual observations (countries) and the categories (3 levels of religion, 3 levels of freedom, 3 levels of democracy and 2 levels of colonialism) are displayed (Figure 3). Individual observations are color coded by group. The discontinuity analysis of the complete data set (no longer broken into groups by variable levels) found 5 groups of countries. The ellipses are drawn using group membership in order to visualize how proximate countries in the same size class are to each other.

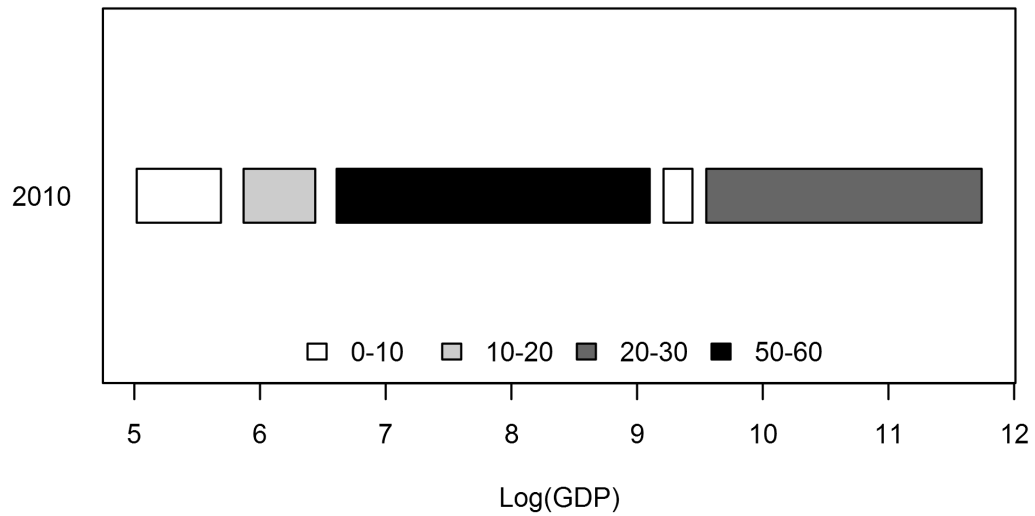


Figure 3.2 Discontinuous structure of the complete distribution of 190 countries. Note how the gaps occur at same location as gaps marked by red vertical lines in Figure 1. Color coding reflects percentage of countries found in each size class.

Free, Christian countries with a High Lifespan cluster closely (left hand side of graph), and are close to Not Colonies with a Medium Lifespan. In the upper right quadrant, Former Colonies and Partially Free countries are close together, and those two variables are also near to two other closely clustered variables, Low Lifespan and Other religion. In the bottom right quadrant, farthest from Free, Christian countries with a High Lifespan, lie Muslim and Not Free countries. However, the ellipses, drawn using the density distribution of countries belonging to the same size class (Group 1, Group 2, etc.), tell a slightly different story. First, it is clear that Group 5, which is the wealthiest grouping of countries, is comprised of countries that are highly similar to each other with regards to their classifications for all 4 variables, as evidenced by the very small ellipse. On the other end of the wealth spectrum is Group 1, and while its ellipse does not overlap that of Group 5 at all, it is much larger, indicating that the countries in that group are more dispersed with higher variance in

their classifications. Nonetheless, the poorest countries fall exclusively on the right side of the graph, associated with less freedom, non-Christian religion, and a lower lifespan. They also tend to be former colonies. The distribution of Group 2, the second-poorest group, also does not overlap with Group 5, has less variance than Group 1, and in fact largely falls inside the density distribution of Group 1, indicating that the countries in that group are more tightly defined by a lower lifespan, less freedom, non-Christian religion, and being a former colony. Group 4, the second-wealthiest group, is almost fully orthogonal to Group 2, and resides strongly on the left side of the graph, dominated by freedom, a high lifespan, not being a colony, and Christianity. Group 3, which falls in the mid-ranges of the wealth spectrum, has the broadest ellipse, encapsulating almost the entire ordination space.

We calculated the percentage of each variable level that fell within each group identified by the discontinuity analysis (Figures 4-7). Democratic freedom is strongly correlated to wealth, as no free countries fall in the poorest group, and only 2% of Free countries fall in Group 2, the second poorest group (Figure 4). Similarly, only 5% of the Not Free countries fall in the wealthiest group, and only 5% of the Partly Free countries fall in the wealthiest two groups.

Religion is similarly stratified (Figure 5). Christian countries tend to fall in the middle of the distribution, skewed toward the wealthy end.

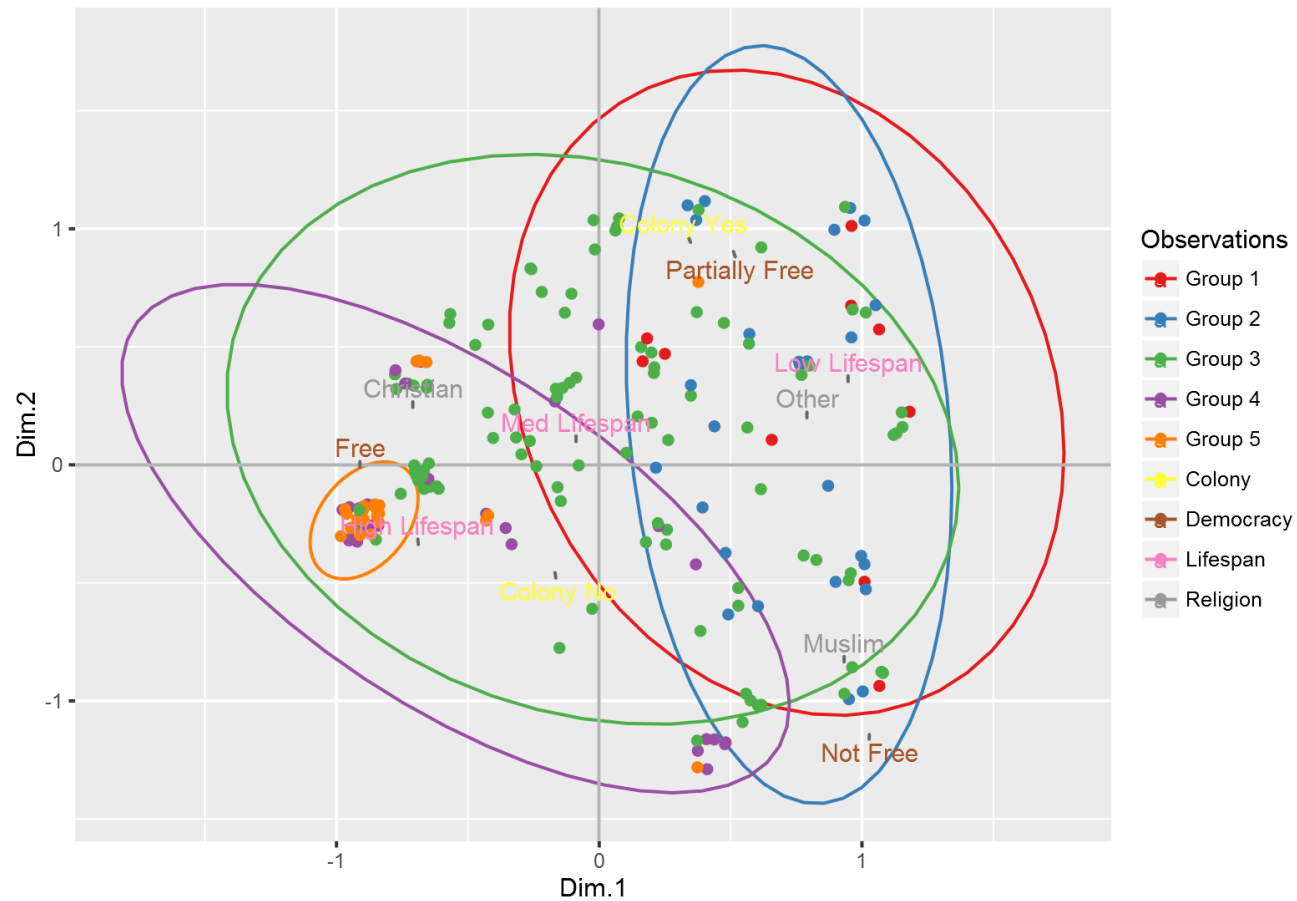


Figure 3.3 Multiple Correspondence Analysis with observations (countries) shown as points and levels of categories as text labels. Ellipses are drawn around each GDP size class to show the relative density of countries within a size class. Group 1 is the poorest, and Group 5 is the wealthiest size class. ([Figure 3.3.pdf](#), 8.8KB)

The non-Christian or Muslim-dominated countries also fall primarily in the middle of the distribution, but are skewed toward the poorest groups (38% in two poorest groups, versus 16% in the two wealthiest groups).

No countries with a High life expectancy fall in the two poorest groups, while no countries with a Low life expectancy fall in the wealthiest group, and only 2% fall in the second wealthiest group (Figure 6). Countries with a Medium life expectancy are overwhelmingly medium in wealth, with no countries in either the richest or poorest group and 84% of the countries in Group 3. Countries with a High life expectancy were not concentrated in the middle of the distribution, but were evenly spread across the 3 wealthiest groups.

Like the other variables, a country's colonization status is correlated with GDP (Figure 7). Not-colonies fall predominately in the middle of the distribution in Group 3, as do former colonies, but are moderately skewed towards the wealthier groups (16% in the two poorest groups, and 36% in the two wealthiest groups), while former colonies are skewed towards the poorer groups (24% in two poorest groups, and 12% in the two wealthiest).

In sum, the distribution of variables across the countries aligns with the MCA, in that countries that fall in a wealthy group are more likely to be Free, Christian, have a High life expectancy and not be a former Colony, whereas countries that are in a poorer group are more likely to be Not Free or Partly Free, Muslim or Other, have a Low life expectancy, and be a former Colony.

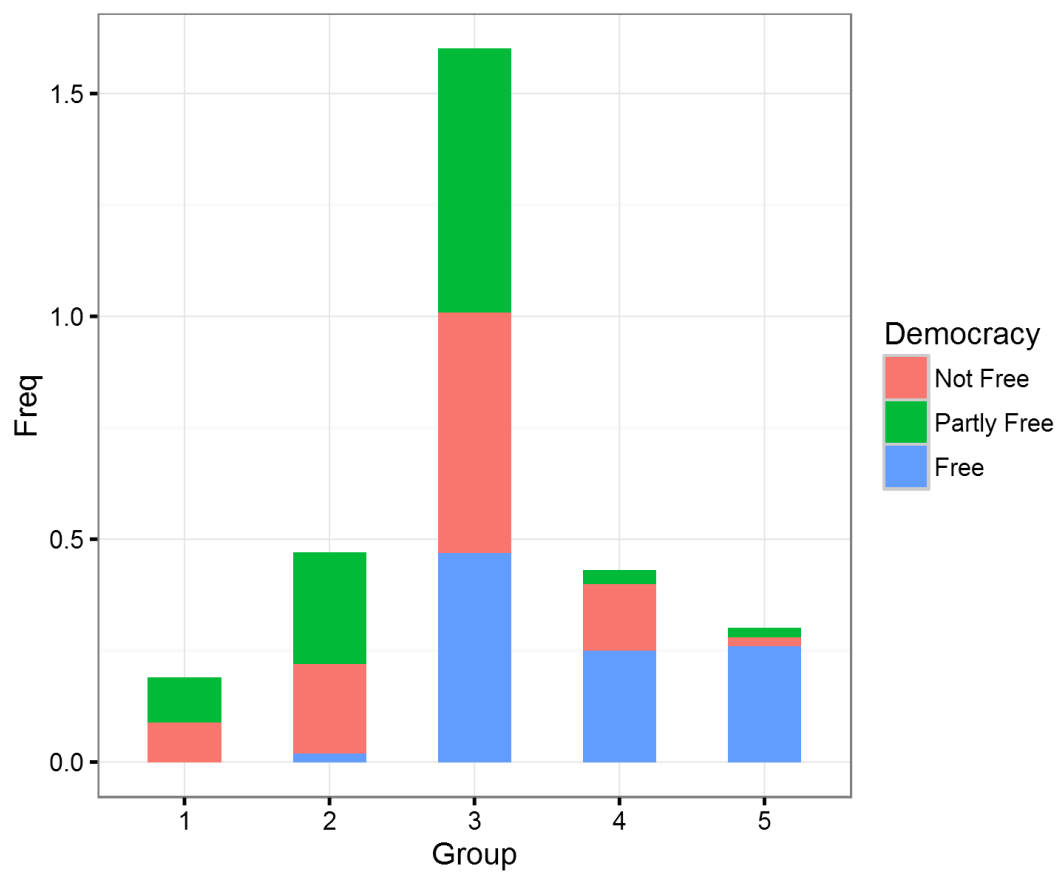


Figure 3.4 The distribution of countries for variable Democracy across the 5 size classes of GDP, where Group 1 has the lowest GDP.

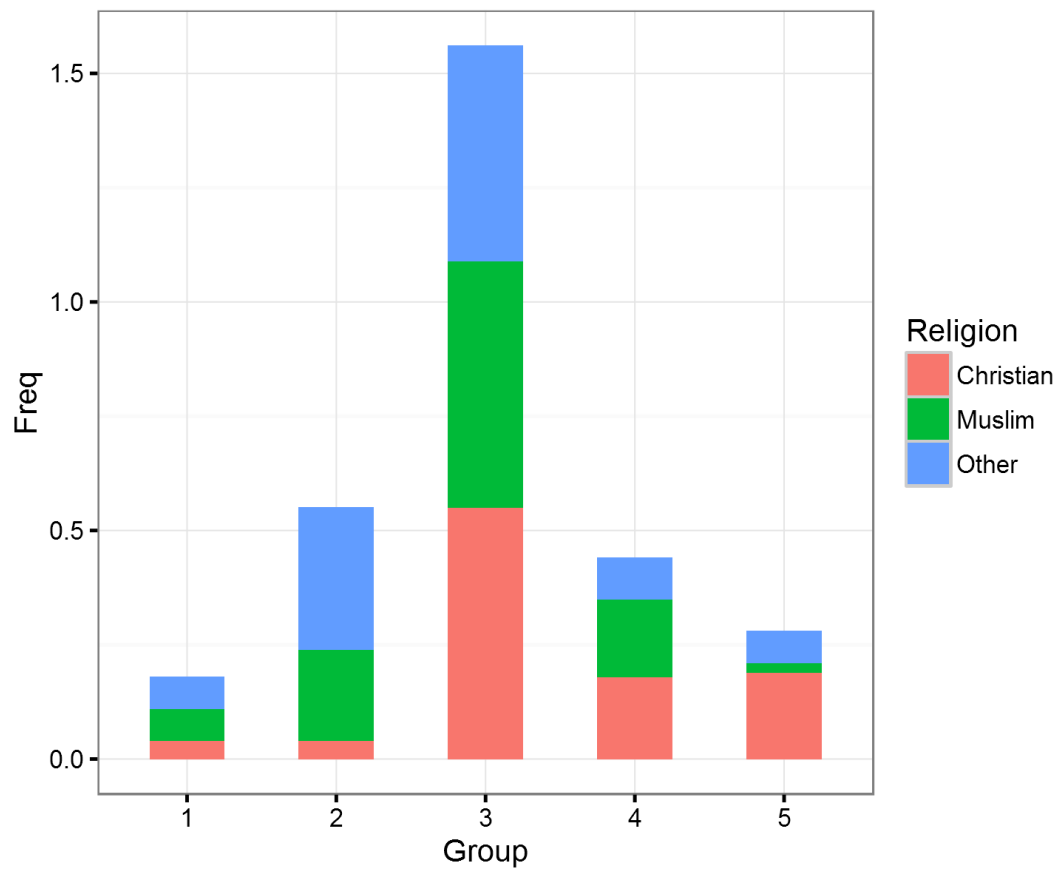


Figure 3.5 The distribution of countries for variable Religion across the 5 size classes, where Group 1 has the lowest GDP.

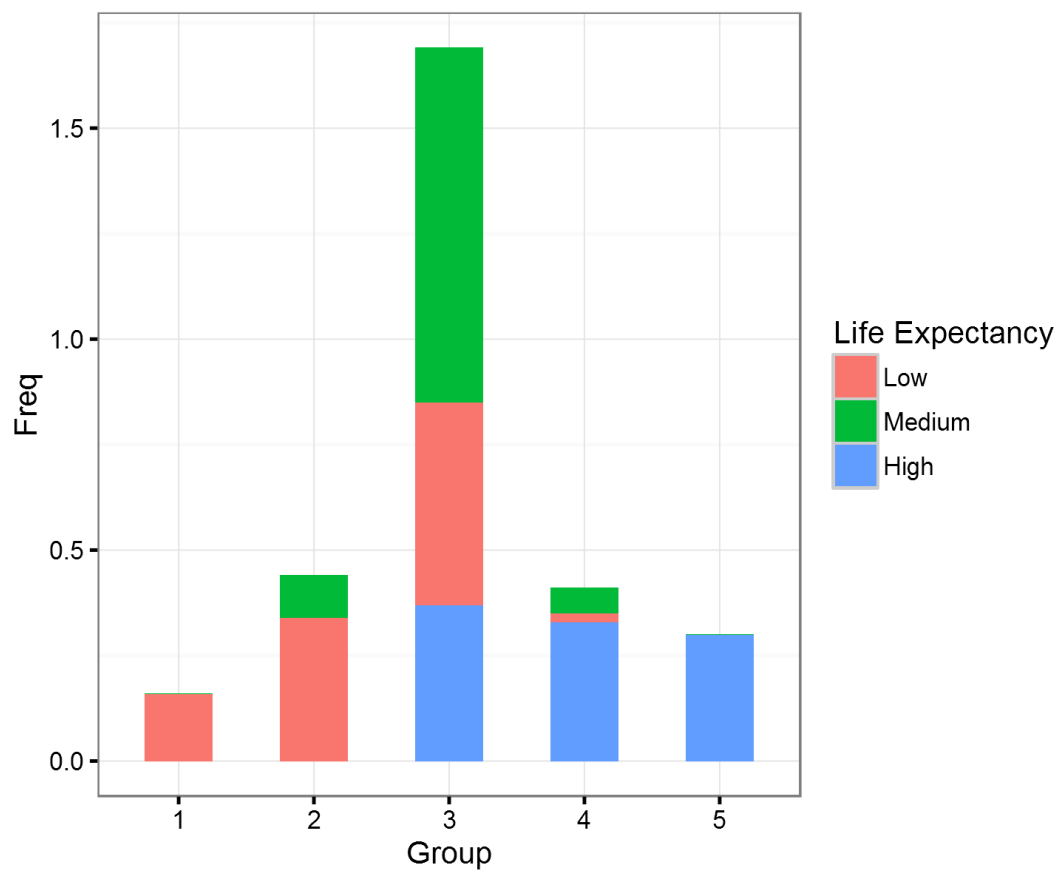


Figure 3.6 The distribution of countries for variable Life Expectancy across the 5 size classes of GDP, where Group 1 has the lowest GDP.

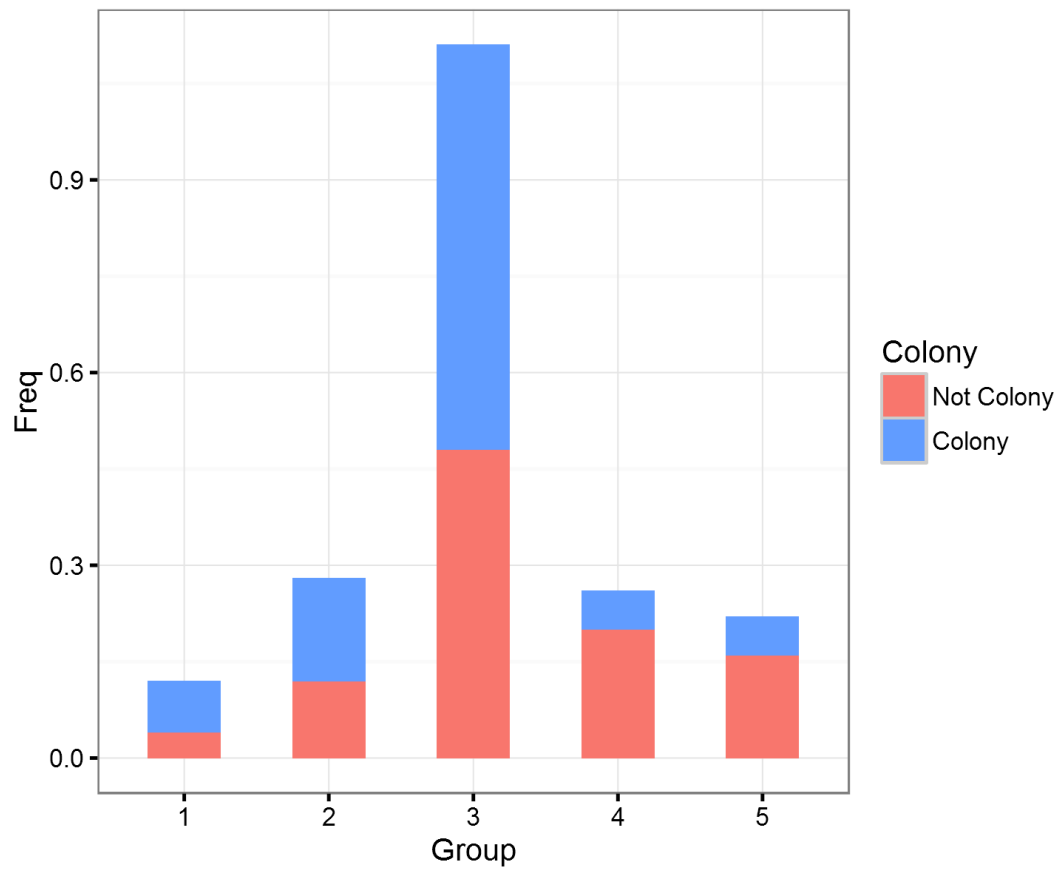


Figure 3.7 The distribution of countries for variable Colony across the 5 size classes of GDP, where Group 1 has the lowest GDP.

Discussion

We tested whether discontinuities in GDP for 190 countries were associated with four cultural variables that have been explored by the economics literature for their relationship to wealth and growth rate, namely, democracy, life expectancy, religion, and colonialism. We did so by evaluating subsets of countries partitioned by their classification for each variable for discontinuities and congruence in gaps. For example, each of the 190 countries was classified for the variable democracy into one of three levels: Free ($n = 85$), Partly Free ($n = 59$), and Not Free ($n = 46$). Each data subset was evaluated for discontinuities, which are non-random gaps in the distribution where no countries fall within that particular range of GDP. Thus, the discontinuous distributions consist of groups of countries with a similar size of GDP, and gaps, where there are no countries. The groups are size classes, endogenously generated from within the global economy and identified objectively by the discontinuity methodology, and are hypothesized to be basins of attraction that represent a particular set of economic opportunities at those spatial and temporal scales. It is presumed that while a number of processes are likely to be responsible for structuring the size classes, or basins, there are likely a few key processes that operate over limited ranges of spatial and temporal scales that play a strong structuring role for each size class. If any of our four variables were one of those key processes, then we would expect it to generate gaps that align across all the levels of a variable.

In general, the results indicated that the distribution of wealth, as captured by GDP, was strongly discontinuous, which is what we would expect in a complex adaptive system due to hierarchy, scaling, and non-linear interactions. Although we

found discontinuities in both the complete distribution and in all 11 data subsets, we did not find strong evidence that these variables are individually operating as primary drivers in structuring all the size classes because the gaps were not congruent across all levels of each variable. The two exceptions were in the Partly Free and Not Free levels of the democracy variable, and the Low and Medium levels of life expectancy, where there were congruent gaps beyond the gaps inherited from the complete dataset (Figure 1). The inconsistent alignment of the gaps across the levels of a variable suggests that while the cultural variables are associated with wealth they are not directly responsible for structuring the size classes at all scales. We cannot, however, reject the possibility that these variables play a role in structuring the size classes, for two reasons. First, there is the possibility that these variables interact with each other and/or other unexplored variables in complex ways to generate the gaps which occur across all the datasets. Regressing these variables with interactions against size class membership would be ideal, but the small n in individual response categories and total number of parameters precludes that as a statistically robust approach. Second, these variables may not operate in the same way across all countries, as other studies have suggested (Yang 2008; Narayan et al. 2011), but play an outsized role at only a limited range of spatial and temporal scales, as is the case in ecosystems (Holling 1992). For example, democracy could play a vital role in maintaining a basin of attraction at the wealthiest end of the scale, but be less relevant in structuring the mid-ranges. In that case, we would not expect to see congruence in gaps across all levels of a variable. Furthermore, similar work on growth rates in city size classes found that it varied by size class; the conclusion was that different processes drive growth at

different size classes. Such a conclusion does not require interactions, just that process varies with scale (Allen et al. 2006; Garmestani et al. 2007).

Disentangling these patterns is not trivial. The rank-ordered distributions used in the discontinuity analysis mean that countries that are not proximate to each other in the distribution in terms of their log GDP will not end up in the same size class, unless there are very few size classes detected. We controlled for population by using per capita GDP, so large and small countries can be found in the same size class, but countries with highly disparate per capita GDP are unlikely to be. This means that the wealthiest countries and the poorest countries will be partitioned by their relative wealth. Since the cultural variables that we used are correlated with wealth, in that wealthier countries are more likely to be democracies, have a high life expectancy and be Christian, it begs the question of whether our results are spurious. We had a specific and novel hypothesis, which asked whether these variables could be responsible for structuring the size classes, which were detected by assumption-free, objective methods that evaluate rank-ordered data for discontinuities. It was possible, therefore, that no discontinuities would be detected, or conversely, that only one discontinuity would be found (which results in two groups, one on either side of the gap), which would align with the ‘twin peaks’ convergence club literature which finds two clubs, one rich and one poor (Quah 1996a). It was also possible that each data subset would be discontinuous but no gaps would align, indicating that other processes were responsible for generating scaling in the global economy but without providing any clues. Instead, all the distributions were discontinuous, but with the exception of two levels of life expectancy (Low and Medium), and two levels of democracy (Not Free and Partly Free), gaps were not congruent across the levels of

the variables, suggesting that these variables are not directly structuring the size classes. However, 4 of the 11 variables did share gaps, which would be an unlikely random outcome.

We did not, however, end our analysis with the analysis of the discontinuities. We also took a reverse approach to evaluate whether or not, given just each country's classifications for the four variables, an unsupervised dimension-reduction technique (MCA) could correctly predict size class membership. If these variables are correlated with wealth, and the size classes are a function of wealth, then there is currently no way to distinguish between a linear correlative relationship between gradients in a variable and wealth, and that variable acting mechanistically to structure wealth. This is akin to the challenges other researchers have faced regarding directionality between these variables and GDP—does religious belief drive GDP, or does GDP generate religious belief (Barro & McCleary 2003)? However, it is clear from the economic literature that while these variables are correlated with wealth, they have a far from simple relationship, with often inconsistent and contradictory results.

Thus, the MCA analysis sheds some light on these complexities, because it demonstrates that these variables have a differential relationship with wealth (Figure 3). The MCA shows that democracy and life expectancy strongly explain membership in the wealthiest size class, as manifested in a very small ellipse for Group 5, the wealthiest group (Figure 3), but was only generally correlated to country membership in the poorest size class. The ellipse for Group 1, the poorest group, encompasses virtually all levels of all variables except for Free, High Lifespan and Christian, whereas if the relationship were linear, we would expect to see an equally

small ellipse for the poorest countries containing Not Free and Low Lifespan. In fact, the ellipse for Group 2, the second poorest size class, is smaller and more strongly correlated with variables that fall on the other end of the spectrum from Free and High Lifespan. While these variables in general appear to be strongly related to being wealthy, they are more loosely related to being poor. Furthermore, if wealth were linearly related to these variables, then we would expect the middle size class to be associated with the mid-ranges of these variables, namely, Partially Free, a Medium life expectancy, and Other religion. Instead, the middle size class is the biggest ellipse of all, encompassing every level of every variable with the exception of Not Free. This suggests that these variables are differentially and non-linearly related to wealth, which means that democracy or life expectancy may well be critical structuring processes for wealthy countries, but less so for less-wealthy countries. This might manifest as gaps that do not align across levels of a variable.

It is also important to note that although gaps were generally not consistent across the levels of the individual variables, there were 4 gaps present across almost all levels of all the variables. These ‘master’ gaps appear to reflect structure in the complete data set (a Narcissus effect) as they align with the gaps detected when the full distribution of 190 countries is analysed for discontinuities. The master gaps provide strong support for the contention that there are processes acting as critical structuring agents and generating size classes in global GDP, leaving as an open question what those processes may be, and whether they are operate at all scales or only a limited range of scales. If the hierarchical structure of economies is similar to ecosystems, it is likely that different structuring processes affect one or a few scales, which in total give rise to a discontinuous distribution.

Furthermore, the master gaps occur in the tails of the data, a pattern that is corroborated by the convergence club literature and our MCA results. The implication is that the basins of attraction are larger, deeper, and more persistent in the tails of the data, and shallower and more ephemeral in the mid-ranges. Within the convergence club literature few researchers have framed their analyses in the language of complex systems, and compared the clubs to basins of attraction. Notably, some of these researchers have used methods that allow for more than two clubs, and find evidence for the presence of multiple clubs in a variety of econometrics (Durlauf & Johnson 1995; Apergis et al. 2012), but even more strikingly, they also find that the mid-ranges of the data tend to be messier than the tails (Battisti & Parmeter 2013; El-Gamal & Ryu 2013). The MCA results show the same pattern. Although only the ellipse for the wealthiest size class is small, the ellipses for the two wealthiest size classes are almost fully orthogonal to and separated from the ellipses for the two poorest size classes, while the ellipse for the middle size class is, as previously noted, expansive, implying that the socio-cultural variables do a poor job of explaining size class membership in the middle of the distribution. This pattern indicates stronger attractors in the tails of the data. Previous research (Sundstrom et al. in review) found that the discontinuous distributions of all countries of the world over 43 years of data had discontinuous pattern that was strongly persistent in the tails of the data over time, with gaps occurring across almost all years of data in the same location, whereas the middle of the distribution showed higher variability on the number and location of gaps. In dynamical systems theory, this suggests that the basins of attraction operating in the middle of the distribution have weaker attractors and are more transient.

Conclusion

The global economy, comprised in this study of 190 national economies, is strongly discontinuous, consisting of groups of countries with a similar per capita GDP. The cultural variables we explored appear to be strongly correlated to the wealthy size classes, moderately correlated to the poorest size classes, and not at all correlated to the mid-ranges. Whether there is a mechanistic rather than associative relationship is unknown, as is the nature of the processes that are structuring the size classes—are they scale specific, scale neutral, or processes that impact all scales but do so differentially? A rule in ecology is that only a small handful of processes structure any given scale domain, or size class (Gunderson and Holling, 2002). Further work that expands the range of variables tested for their association with the size classes to include econometric variables would hopefully shed light on the processes structuring them.

CHAPTER 4 CROSS-SCALE RESILIENCE IN THE HAWAIIAN ARCHIPELAGO

Introduction

The cross-scale resilience model was proposed as a method to account for diversity, and particularly functional diversity, in measures of ecological resilience (Peterson et al. 1998). Ecological resilience emerges from a multiplicity of ecosystem attributes, including adaptive capacity and response diversity, so the cross-scale resilience model captures only a portion of the system attributes that underpin resilience (Elmqvist et al. 2003; Allen & Holling 2010). The relative importance of functional diversity for ecosystem persistence and function has been validated in non-resilience related ecological studies that have their roots in the extensive debate on the value of biodiversity (Tilman et al. 1997; Symstad & Tilman 2001; Díaz et al. 2007). The outcome of that debate has confirmed that richness and redundancy in functional traits as expressed by species are critical for ecosystem productivity, persistence, and vulnerability to disturbances (Mouillot et al. 2013b; Gagic et al. 2015; Cadotte 2017).

The merits of measuring functional diversity are therefore clear, as there are increasingly strong mechanistic links between functional diversity and ecosystem-level attributes. The functional diversity literature is now well-developed, and classic biodiversity metrics such as diversity and evenness have been adapted, expanded, and validated as a means of measuring functional diversity (Hubálek 2000; Villéger et al. 2008; Laliberté & Legendre 2010; Santini et al. 2017). Univariate categorical traits that require species' *a priori* classification into functional groups have been replaced

by sophisticated continuous multi-trait metrics that cluster species according to their trait expression (Villéger et al. 2008; Petchey et al. 2009). What is not accounted for in these diversity evaluations, however, is scale.

The strength of the cross-scale resilience model therefore still lies in its explicit articulation of the scales at which species' functionality is expressed. There is no longer any question that functional diversity plays a critical role in ecosystem-level attributes that are of interest, such as resilience and productivity. But the degree to which it is valuable or necessary to understand how functional diversity is distributed within and across the scales of a given system remains less examined.

I used coral reef fish community data from the Hawaiian archipelago to examine whether the cross-scale resilience of fish communities that come from different regions within the archipelago, or from reefs that are dominated by different regimes, have the same cross-scale resilience. My expectation was that the cross-scale structure will systematically differ both between regions and among reef regimes and will be higher in the northwestern Hawaiian islands, and for communities found on coral-dominated reef.

Material and Methods

Study area

The Hawaiian archipelago consists of a string of islands that are highly isolated from any continent. The main Hawaiian islands (MHI) and the northwestern Hawaiian islands (NWHI) are considered two distinct regions within the archipelago because the MHI are heavily populated and the reefs are subject to a variety of anthropogenic disturbances, including overfishing and pollution (Williams et al. 2011;

Friedlander et al. 2013), whereas the NWHI are considered relatively pristine as the area is unpopulated, formally protected, and free of any localized anthropogenic disturbances (Kittinger et al. 2011).

Data

All data were manipulated and analysed in R v. 3.4.2 (R Development Core Team 2016) with the exception of the Gap Rarity Index. Specific packages used are referenced in the text.

Coral reef fish data came from a large-scale monitoring program in the Western Central Pacific ocean collected as part of the NOAA Pacific Reef Assessment and Monitoring Program (PRAMP) and supplemented by additional survey efforts led by Papahānaumokuākea Marine National Monument (PMNM), using identical methods and design (Heenan et al. 2017). Fish data were collected in 2010 from 302 sites across 11 islands. Hawai'i, Kaua'i, Lāna'i, Maui, Moloka'i, Ni'ihau, and O'ahu are part of the MHI, and French Frigate Shoals, Kure, Lisianski, and Pearl & Hermes are from the NWHI (Figure 1).

Reef sampling was limited to hard-bottom substrate in < 30 meters of water. Sampling sites were chosen randomly prior to the survey cruise, and the number of sites per island were proportional to reef size. Surveys were conducted using underwater visual counts in the form of a stationary point count where pairs of divers conduct simultaneous counts in adjacent 15 meter cylindrical plots (see McCoy *et al.* 2016 for detailed survey method), and length of fish to the nearest cm was recorded. Fish were converted to biomass using the appropriate length-length conversion if necessary, followed by the length-biomass conversion. Conversion metrics primarily came from Fishbase (Froese & Pauly 2017) and Kulbicki et al. (2005) while a few

were developed by PRAMP for fish classified to the genus or family level. Trophic level classification came from the PRAMP database.

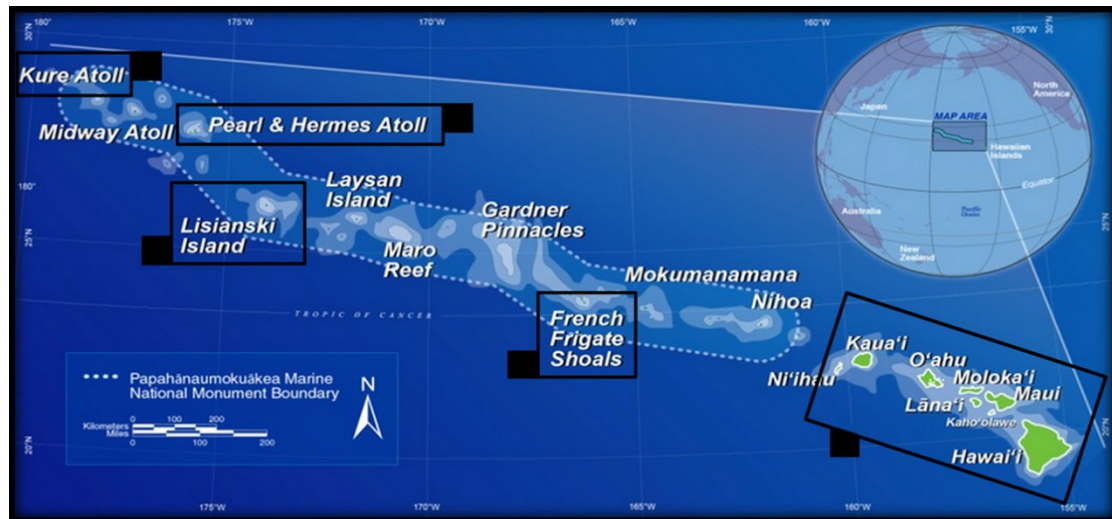


Figure 4.1 Map of the study area. Islands in the lower-right block belong to the main Hawaiian islands, while the remaining islands are part of the northwestern Hawaiian islands (from Jouffrey et al. 2014).

Sampling data were pooled by island using site regime classifications from Jouffray et al. (2014), who classified each of the 302 sampling sites into either coral, turf, or macro algae benthic reef regime. Macro algae and turf sites were pooled together, as those regimes were more similar to each other than to the coral regime (Jouffray et al. 2014). Each island therefore had two fish community data sets, one for all fish from coral-dominated sites, and one for all fish from macro algae and turf-dominated sites. The island of Ni'ihau did not have any coral sites, leaving a total of 21 community data sets. Data for each community consisted of a list of fish species, their regional maximum body size, and their classification by trophic level. Regional maximum body size for each species was compiled by recording the largest observed fish for each species from all fish sampled during 2010-2016 at the same 11 islands

by PRAMP. Regional maximum size was used instead of maximum observed body size in FishBase because many of the FishBase observations were recorded in the 1700's or 1800's and come from all over the world, so may represent an unrealistic standard for fish size in the western central Pacific given changes to coral reef fish habitat in the last century and differences between habitats around the globe. The regional maximum body size and maximum observed body size distributions were significantly different (p-value from Wilcoxin paired test < 0.001).

As species richness is a function of area sampled (Gotelli & Colwell 2001) and larger reefs were more heavily sampled than smaller reefs, I used sample-based rarefaction analysis (package 'vegan') to ensure that sampling was sufficient to allow among-site comparison. Rarefaction is a specialized form of species accumulation curve that standardizes data sets by repeatedly resampling the pool of samples without replacement (Gotelli & Colwell 2001). Sites can only be validly compared if the rarefaction curve asymptotes. Rarefaction curves were computed on functional diversity rather than species diversity, as that is the base metric used in the analysis. All sites minus one clearly asymptoted, and as that site was nearly at an asymptote it was retained in the analysis.

Cross-scale resilience

The cross-scale resilience model equates a resilient distribution of functional diversity emerges from the overlapping diversity of functions within a scale domain, and the redundancy of functions across scale domains (Peterson et al. 1998). As the first step in an analysis, it is necessary to identify the scale domains of a system. I followed the established methodology in the literature (Holling 1992; Sundstrom et al. 2012; Nash et al. 2014a) and identified the scale domains for each of the 21

communities with the Gap Rarity Index (GRI) on rank-ordered log transformed fish biomass. The GRI compares the observed size distribution with a continuous unimodal null distribution generated by smoothing the observed data with a kernel density estimator (Silverman 1981). The null distribution is sampled 4000 times in a Monte Carlo procedure and the probability that the observed discontinuities in the size distribution occur by chance is calculated as a GRI statistic and tested for significance. The coral community from Kaua'i was dropped from the analysis as it had 8 species, which is an insufficient sample size for the GRI.

Metrics of cross-scale resilience

Three metrics were used to capture the distribution of functions within and across scales (Allen et al. 2005). Average functional group richness is the average number of functional groups in each scale domain. Within-scale redundancy is the average number of species per functional group per scale domain. Cross-scale redundancy is the average number of scale domains at which a functional group is represented.

Statistical analysis

Communities were compared using a factorial MANOVA, with region (MHI and NWHI) and regime (coral and macro-turf) as two-level independent factors, and average functional group richness, within-scale redundancy and cross-scale redundancy as response variables. Island was designated as a random effect to account for the possibility that variation within an island was higher than variation among islands. A Spearman rank correlation coefficient showed only a moderate correlation between average functional group richness and within-scale redundancy

(0.65), and the data passed all assumptions of a MANOVA, which are outliers (pkg ‘mvoutlier’); multivariate normality (Shapiro-Wilk pkg ‘mvnormtest’); homogeneity of variances (Fligner-Killeen base pkg), and homogeneity of covariance matrices (boxM pkg ‘biotools’).

Results

A basic exploration of the data reveals the relationships between the species attributes of richness, functional richness, and number of scale domains with the independent variables of region and regime. There were 20 community data sets, as each of the 11 islands had a ‘community’ representing all coral sites pooled and all macro-turf sites pooled, except for Kaua’i and Ni’ihau. Species richness ranged from 43 to 126 species; the number of scale domains detected ranged from 5-10; and the number of functional groups ranged from 9 to 11 (Table 1). As expected, the number of functional groups increases with the number of species (Figure 2).

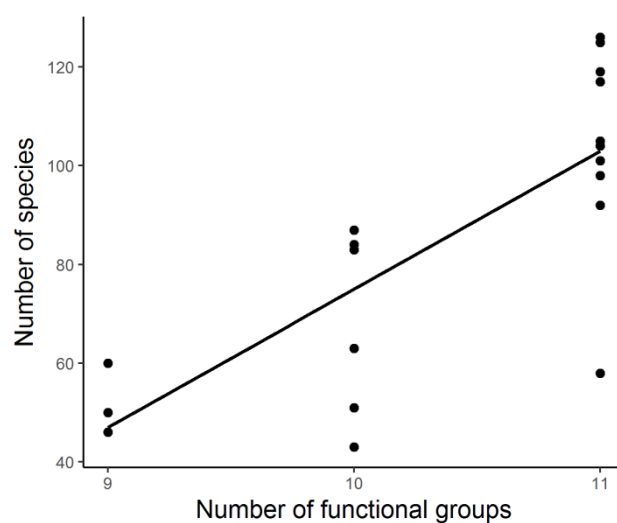


Figure 4.2 Relationship between species richness and functional groups for all reef fish communities.

Table 4.1 Fish community metrics of the Hawaiian archipelago. Regions are main Hawaiian islands and northwestern Hawaiian islands; Regimes are coral or macro-turf; FG = functional group.

Region	Island	Regime	# of species	# of scale domains	# of FG's	Cross-scale redundancy	Avg # of FG's per scale	Within-scale redundancy
MHI	Hawaii	C	101	8	11	3.82	5.25	2.43
MHI	Lanai	C	63	9	10	3.90	4.22	1.72
MHI	Maui	C	84	7	10	3.70	5.29	2.21
MHI	Molokai	C	60	8	9	3.78	4.25	1.66
MHI	Oahu	C	46	8	9	3.33	3.75	1.47
MHI	Hawaii	MT	125	9	11	4.45	5.44	2.56
MHI	Kauai	MT	126	7	11	3.36	5.29	3.46
MHI	Lanai	MT	87	8	10	3.40	4.25	2.49
MHI	Maui	MT	117	9	11	4.18	5.11	2.53
MHI	Molokai	MT	51	8	10	2.50	3.13	2.17
MHI	Niihau	MT	105	6	11	2.82	5.17	3.20
MHI	Oahu	MT	104	5	11	3.00	6.00	2.39
NWHI	French Frigate Shoals	C	83	8	10	3.20	4.00	2.40
NWHI	Kure	C	58	7	11	3.00	4.71	1.68
NWHI	Lisianski	C	84	10	10	4.30	4.30	1.99
NWHI	Pearl & Hermes	C	43	7	10	2.70	3.86	1.72
NWHI	French Frigate Shoals	MT	92	6	11	3.00	5.50	2.73
NWHI	Kure	MT	98	5	11	2.91	6.40	2.89
NWHI	Lisianski	MT	50	7	9	3.00	3.86	1.90
NWHI	Pearl & Hermes	MT	119	8	11	3.55	4.88	3.21

The relationships between region and regime and the number of species, number of functional groups, and number of scale domains are largely insignificant.

Communities from a macro-turf regime have more species and more functional groups, but there is little difference between regimes or regions for the other species attributes (Figure 3).

An initial MANOVA found a significant multivariate effect for regime and island, but not region (Table 2). The relationships between region and regime and the three cross-scale metrics are largely insignificant in visual inspections via boxplots (Figure 4). Univariate analyses for the effect of regime and island for each of the response variables found the effect to be significant only for within-scale redundancy (Table 3). In other words, within-scale redundancy varied between islands and within islands, and was higher for communities from a macro-turf regime (Figure 5).

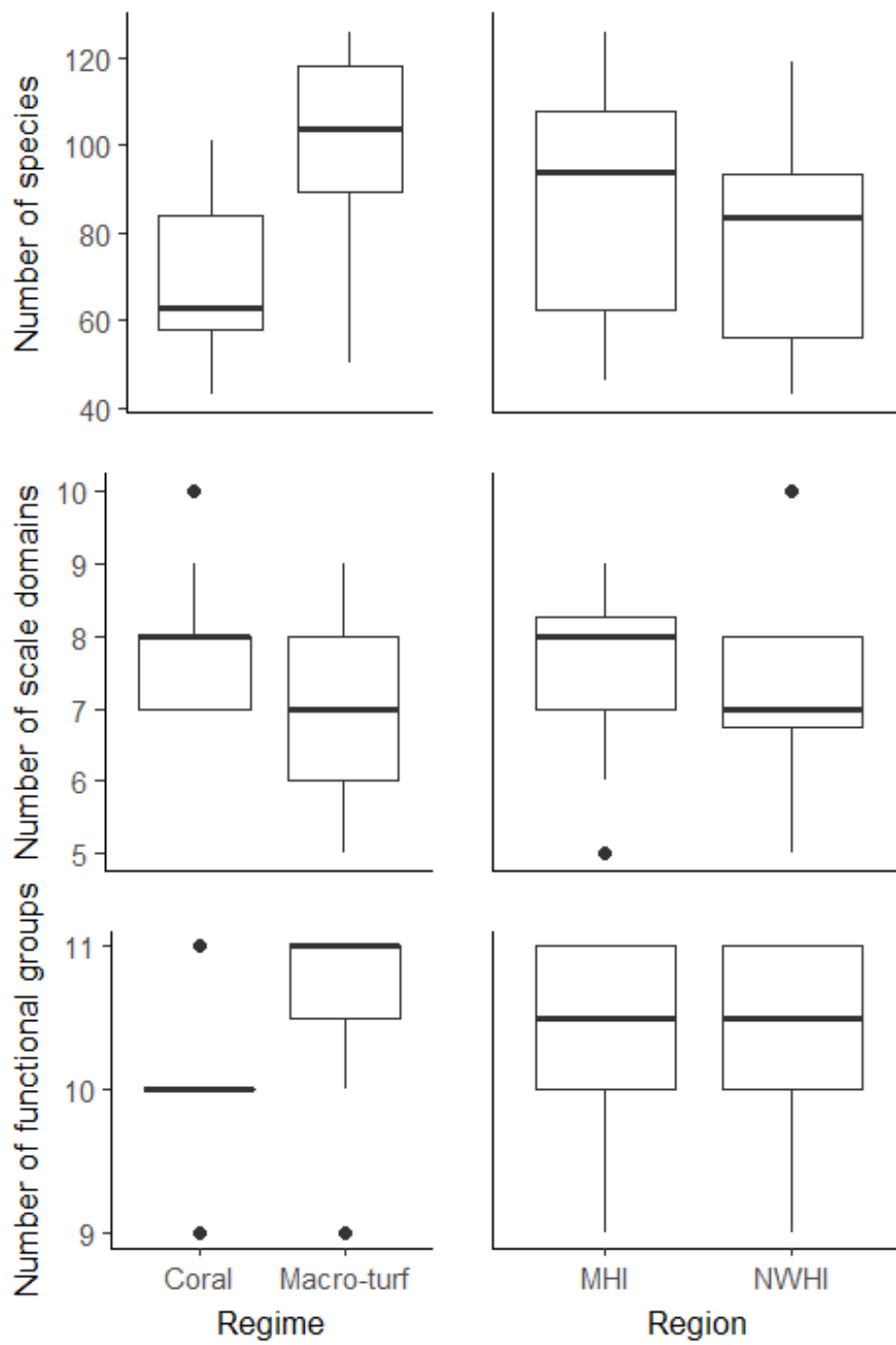


Figure 4.3 Boxplots for differences in median values of three descriptive measures for coral and macro-turf regimes, and the main Hawaiian islands (MHI) and northwestern Hawaiian islands (NWHI).

Table 4.2 MANOVA results comparing cross-scale resilience metrics between regions, and between regimes, both within islands and among islands.

Error: Island	Df	Pillai	approx F	num Df	den Df	Pr(>F)
Region	1	0.175	0.424	3	6	0.743
Regime	1	0.794	7.715	3	6	0.018 *
Residuals	8					
Error: Within	Df	Pillai	approx F	num Df	den Df	Pr(>F)
Regime	1	0.689	4.4204	3	6	0.058 .
Residuals	8					

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 4.3 ANOVA results testing for significant differences in each cross-scale metric between regimes, both within islands and across islands.

Error: Island	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Response Cross-scale redundancy					
Regime	1	0.206	0.206	0.611	0.455
Residuals	9	3.029	0.337		
Response Average # functional groups per scale domain					
Regime	1	0.542	0.542	0.769	0.403
Residuals	9	6.344	0.705		
Response Within-scale redundancy					
Regime	1	2.172	2.172	17.294	0.002 **
Residuals	9	1.131	0.126		
Error: Within	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Response Cross-scale redundancy					
Regime	1	0.168	0.168	0.566	0.474
Residuals	8	2.374	0.297		
Response Average # functional groups per scale domain					
Regime	1	1.352	1.352	2.160	0.180
Residuals	8	5.008	0.626		
Response Within-scale redundancy					
Regime	1	1.721	1.721	12.803	0.007 **
Residuals	8	1.075	0.134		

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

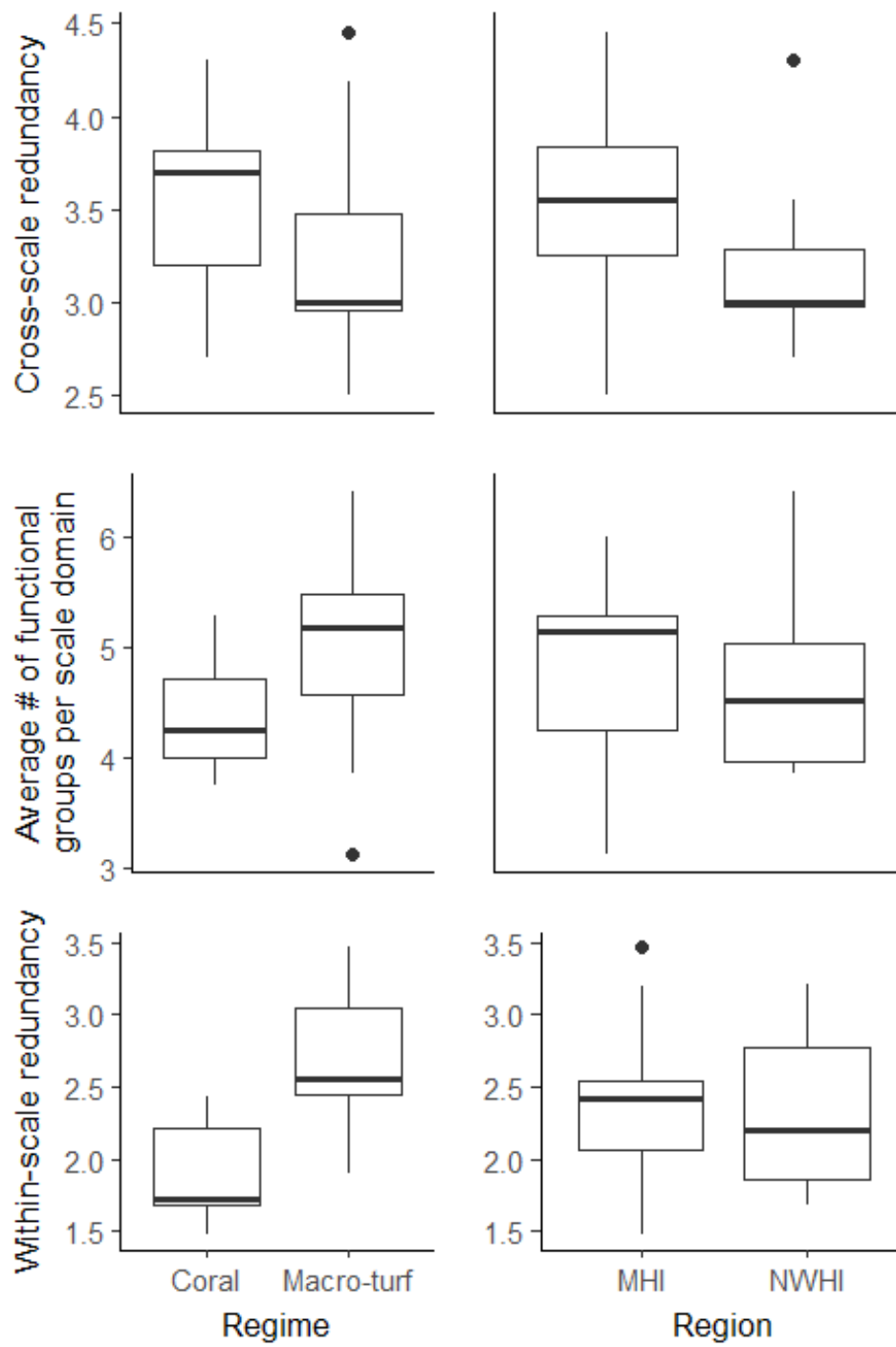


Figure 4.4 Boxplots for differences in median values of the three cross-scale metrics for coral and macro-turf regimes, and the main Hawaiian islands (MHI) and northwestern Hawaiian islands (NWHI).

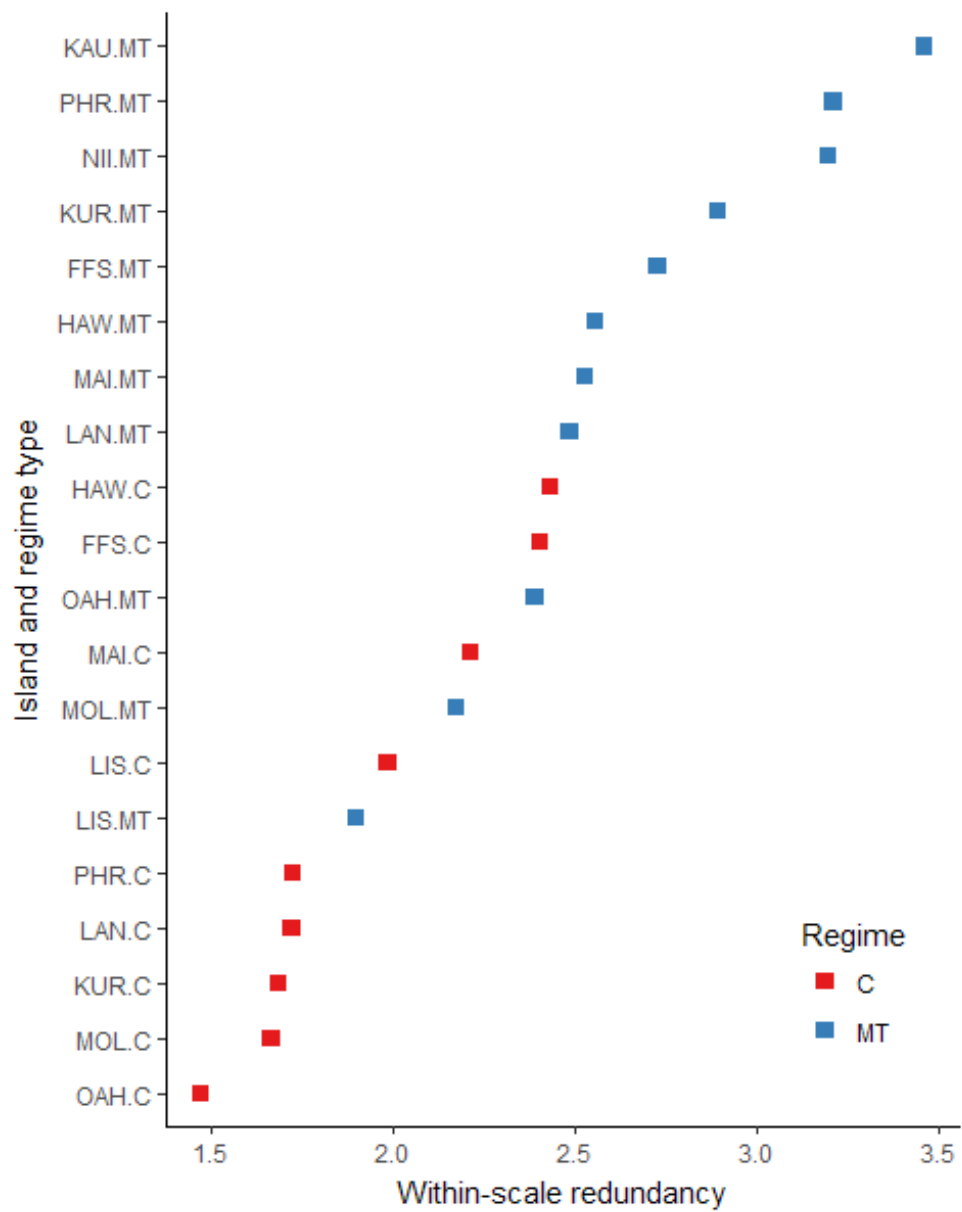


Figure 4.5 Comparison of the within-scale redundancy for each community, coded by regime type. Red squares indicate a coral regime, while blue squares indicate a macro-turf regime.

Discussion

The results of the MANOVA suggest that there were no differences in cross-scale resilience between the two regions, and only a limited difference between regimes or islands. The only significant effect found was within and between islands, and the univariate ANOVA's determined that only one of the three cross-scale metrics had a significant relationship, within-scale redundancy. Within-scale redundancy calculated the amount of functional redundancy within a scale domain and was higher for macro-turf communities, even when within-island variation was controlled for. Reef fish communities dominated by macro algae or turf had, on average, a higher functional redundancy within each scale domain than reef fish communities found on coral-dominated reef.

This is an unexpected result for a number of reasons. The null hypothesis was that cross-scale resilience would be higher in islands belonging to the northwestern Hawaiian islands, and among coral-dominated communities. By a variety of criteria, the NWHI region is less disturbed than the MHI (Friedlander et al. 2013), and remote islands in general support up to three to four times more standing biomass of reef fish (Sandin et al. 2008; Williams et al. 2015). Friedlander et al. (2013) found that differences in density, size and biomass of reef fish communities was 260% higher in the NWHI compared to the MHI. Interestingly, Cinner et al. (2016) found that some sites sampled in both the MHI and NWHI had significantly less fish biomass than expected given the environmental and socioeconomic conditions they are exposed to, suggesting that factors that either interact in unexpected ways or are currently unaccounted for are impacting reef communities. All these studies were assessing biomass, and higher biomass in the NWHI is almost completely due to larger-bodied

apex predators (Friedlander et al. 2013). As my analysis did not include abundance but rather functional group representation, even having just one fish sampled that belongs to a rare functional group such as large predators is sufficient to count in the tally of functional groups at that scale domain, so will influence average functional richness per scale domain and cross-scale redundancy. For within-scale redundancy to be impacted, there would need to be a second observation of a large predator belonging to a different species. Failing to account for abundance is a weakness of this method, but the metric most robust to this is, in fact, the metric which was significantly different between islands and regimes.

Comparing regions may have been confounded by the loss of the Ni'ihau and Kaua'i coral communities from the data set, further unbalancing the number of communities between the two regions. Ni'ihau was removed because it had no coral sites, and Kaua'i was removed because it had only one sampling location that was coral dominated, and only 8 species recorded which is insufficient for the GRI. The absence of coral sites in the MHI was not accounted for in the analysis, and although it may not be statistically significant in the sense that more islands were sampled in the MHI, it is interesting that both of the islands lacking coral dominated communities were from the MHI. It is also possible that comparisons between regions may not be appropriate even though in general, remote reefs typically have both more standing biomass and larger-bodied taxa. Differences in non-human related environmental variables such as oceanic productivity, wave energy and sea surface temperature can significantly impact the ability of a reef to support reef stocks (Williams et al. 2015; Robinson et al. 2017). Finally, coral-dominated reefs are also believed to represent a less disturbed and more pristine system than their macro algae or turf-dominated reef

counterparts. The lack of significant difference in the means of average functional richness per scale domain and cross-scale redundancy between regions, regimes, or islands is therefore surprising. There are two primary ways by which we might reinterpret these results. The first is to question the soundness of the original hypothesis, and the second is to consider what ‘resilience’ means in the specific context of the Hawaiian archipelago.

Assumptions of the analysis

I assumed that the NWHI is a more pristine ecosystem as a result of experiencing little to no human population, and therefore experiencing little to no localized anthropogenic disturbances such as fishing pressure or pollution from nearby landmasses (Williams et al. 2011; Friedlander et al. 2013). However, it should be noted that the original analysis classifying the 302 sampling sites into regimes found that ~ 50% of all sites were turf-dominated sites, across both the MHI and NWHI (Jouffray et al. 2014). This suggests that disturbances driving habitat regime are occurring throughout the archipelago. Turf-dominated reef occurs when macro algae are grazed and there is natural coral mortality (Mumby et al. 2007). The ability of coral to recruit and overgrow turf algae is naturally slow, and becomes even slower when nutrients are elevated, giving turf algae a competitive advantage under conditions of nutrient enrichment (Vermeij et al. 2010). The prevalence of turf sites throughout the archipelago suggests that a combination of nutrient enrichment in the MHI and increased coral mortality across the archipelago could drive increased turf sites. Despite being extremely remote from localized anthropogenic pressures, the NWHI reefs may nonetheless be diminished in their cross-scale resilience as a result of more globalized disturbances such as ocean acidification and increasing sea surface

temperatures. Finally, another factor that may account for a failure to find differences between the regions may be that not all remote reefs support equally high fish biomass, as the very remote northern US Line Islands had almost two and half times the biomass of the equally remote NWHI (Williams et al. 2015).

Other assumptions concerned the relationship between the cross-scale metrics and coral reef regimes. Coral-dominated reefs are associated with increased habitat complexity compared to macro algae or turf-dominated reefs (Nash et al. 2013b; Jouffray et al. 2014). In fact, our sites were classified into regimes by Jouffray et al. (2014) using a Principle Components Analysis that showed a clear relationship between high coral cover, high crustose coralline algae cover, and high structural complexity. We assumed, therefore, that because coral habitat has more habitat complexity than macro algae or turf habitat, there would also be more scale domains detected in those fish community distributions (Nash et al. 2013b, 2014b). An operating assumption of the discontinuity hypothesis, verified by empirical evidence, is that the number of scale domains found in animal communities is analogous to habitat complexity, because discontinuities in animal distributions reflects scale domains in ecological structure (Polo & Carrascal 1999; Haskell et al. 2002; Szabó & Meszéna 2006; Fisher et al. 2011; Nash et al. 2013b; Stirnemann et al. 2015). Animal body size is used as a proxy to detect scale domains in ecological structure because of the difficulty in measuring structure, but one of the only studies that successfully analysed structure for discontinuities did so on coral reefs, and found that the number of scale domains found in reef structure was correlated to the number of modes found in fish size distributions (Nash et al. 2013b). Modes are merely another way to find scale domains in fish size distributions, so are fully analogous to our approach of

finding breaks in rank-ordered size data. We also expect that habitat complexity is positively related to species richness and functional group richness (which are strongly correlated to each other). Therefore, we would expect coral habitat to have more scale domains, higher species richness, and higher functional richness, which should translate into higher values for all three cross-scale metrics.

Indeed, our coral reef fish communities had on average more scale domains than the macro-turf communities (Figure 2), but the relationship was insignificant (Wilcoxin rank sum test, $p > 0.05$). However, Nash et al. (2013b) found that the relative abundance of fish in a mode was more correlated to habitat structure than was the number of modes (scale domains) in a fish distribution. As we did not use abundance when detecting our scale domains, we cannot know if abundance within scale domains has a stronger relationship with degraded and un-degraded sites than the actual number of scale domains detected. An inspection of the abundance of fish sampled at each community reveals that while two sites in the NWHI had the highest abundance of fish sampled, they were both macro-turf sites (Figure 6). Not only was there no significant difference in the abundance of fish between the MHI and NWHI (Figure 7) (Wilcoxin rank sum test, $p = 0.7135$), macro-turf sites had significantly greater average abundance than coral-dominated sites (Figure 8) (Wilcoxin signed rank test, $p = 0.02$). Given that there was an even distribution of both macro algae and turf sites between the two regions (Jouffray et al. 2014), it would appear that there is a robust pattern of greater fish abundance sampled at macro-turf sites than at coral sites.

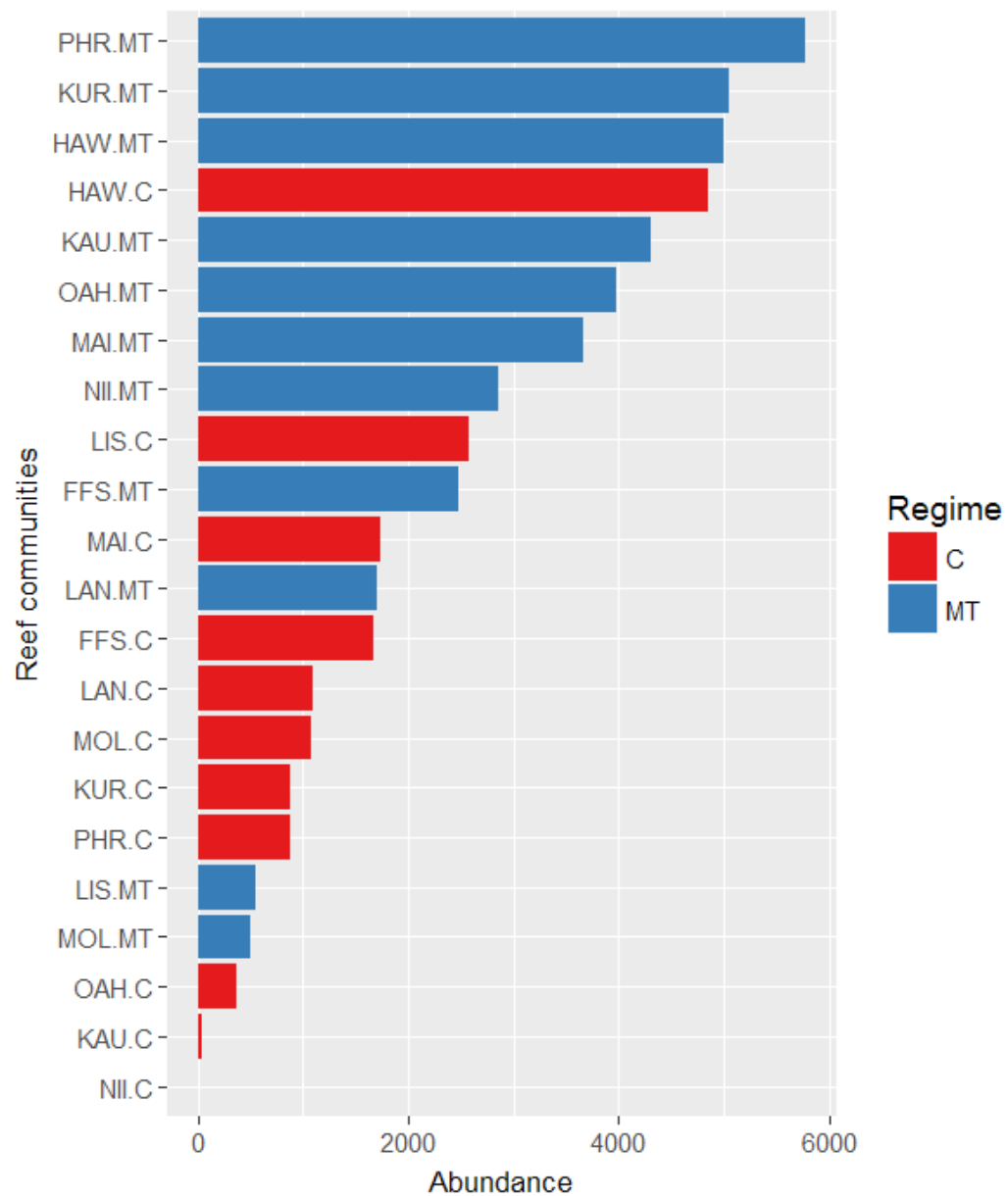


Figure 4.6 Abundance of individual fish sampled from reef communities across the MHI and NWHI. Communities from a coral regime are in red, and communities from macro-turf regimes are in blue.

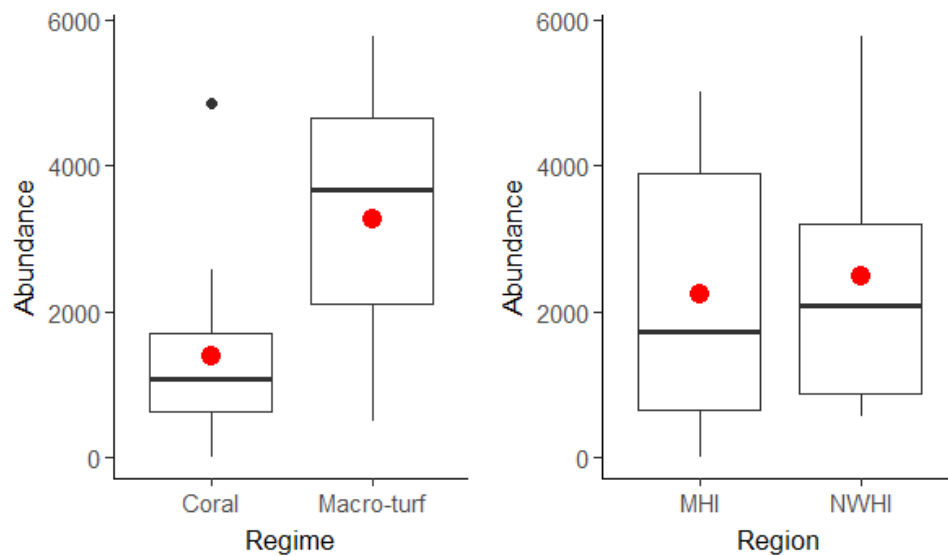


Figure 4.7 Boxplots comparing median values of abundance of individual fish sampled from coral and macro-turf sites (left), and from the MHI and NWHI (right). Means are indicated with red circles.

As for the assumptions that coral habitat would be associated with higher functional richness, and higher means for the three cross-scale metrics, none of them hold up. For example, functional richness is higher for macro-turf sites (Wilcoxin rank sum test, $p < 0.05$), and the greater abundance at macro-turf sites is not biasing our results because sampling rarefaction curves for functional diversity almost uniformly asymptoted. More sampling would not result in finding more functional groups within a community. There is no relationship between cross-scale redundancy and average number of functional groups per scale domain and either regime or region (Figure 3). As none of the three metrics are weighted by the number of scale domains present, they are neither biased by scale domains, nor are they taking into account the number of scale domains. They merely calculate each metric at each scale domain and then average across all scales to attain a community-level average. This may be a weakness of the current method given the expectation that habitat complexity equals more scale domains and thus could be a temporal measure of

degradation. It would appear that my expectations are wrong on two counts: in most cases, there is no relationship at all between regime and region and the cross-scale metrics for the archipelago, and in the one instance in which there is a relationship, it is in the opposite direction as that expected: macro-turf sites have a higher within-scale redundancy than do coral sites, both within an island and among islands.

This brings us to the second assumption about resilience of what, and to what. I assumed that the difference in anthropogenic disturbances would manifest in higher values for the cross-scale metrics in the less disturbed sites. I assumed that the *given* resilience of an ‘untouched’ community would be higher than the *reduced* resilience of a highly disturbed community. Instead it would appear that the conversion of hard coral habitat to a macro algae/turf dominated regime has generated an increased resilience in these sites as manifested by a greater within-scale redundancy of function. It is interesting to note that when comparing coral and turf communities, most of the macro-turf functional groups have higher degree of within-scale redundancy across multiple scale domains (Figure 8). Each observation is the abundance for an island community (i.e. French Frigate Shoals coral community is a red point, and French Frigate Shoals macro-turf community is a blue point). If we just consider the three herbivorous groups, browsers, grazers, and scrapers (Figure 8), we can see that browsers and scrapers tend to occur only at larger scale domains, and grazers tend not to occur at the largest scale domains. Herbivory has long been argued to play a key role in maintaining hard coral reefs in that state (Knowlton 1992; Hughes 1994) and reduced herbivory is correlated to local changes in reef regime (Williams et al. 2001). There is evidence from mid-depth reefs in the Caribbean that although biomass of grazers was positively associated with *cropped* turf and

macroalgal cover, it was negatively correlated with macroalgal cover as there simply weren't enough grazers to maintain the reef in a cropped state (Williams & Polunin 2001). The implications for cross-scale resilience are unclear because biomass and the cross-scale metrics are assessing different attributes, but one possibility is that macroalgae and turf-dominated sites may support a higher functional diversity and redundancy in herbivorous fishes, even if their biomass is insufficient to return the site to a hard-coral dominated regime.

Interestingly, there are also more large invertivores (Large IF), planktivores, small invertivores (small IF), and small predators (SmallPred) in macro-turf communities, although this effect does not hold at the largest scale domains. This suggests that coral reef communities have more within-scale redundancy at the largest scale domains, and this is reinforced by the large predator (Large Pred) observations in which coral reefs have large predators present at larger scale domains than macro-turf communities. It is not possible to know the mechanism in this specific context for this disparity between coral and macro-turf communities at the larger scale domains. Does coral habitat support larger-sized fish, or does the presence of larger-sized fish prevent coral habitat from becoming macro algae or turf dominated? In general, a reduced abundance of fish in larger size classes as evidenced by a less steep size spectra is correlated to human population density and access to markets to sell fish, but the relationship is less significant between regions in the Hawaiian archipelago than within the MHI (Robinson et al. 2017), which may be why we see only minor differences in the functional redundancy at large scale domains between coral and macro-turf regimes.

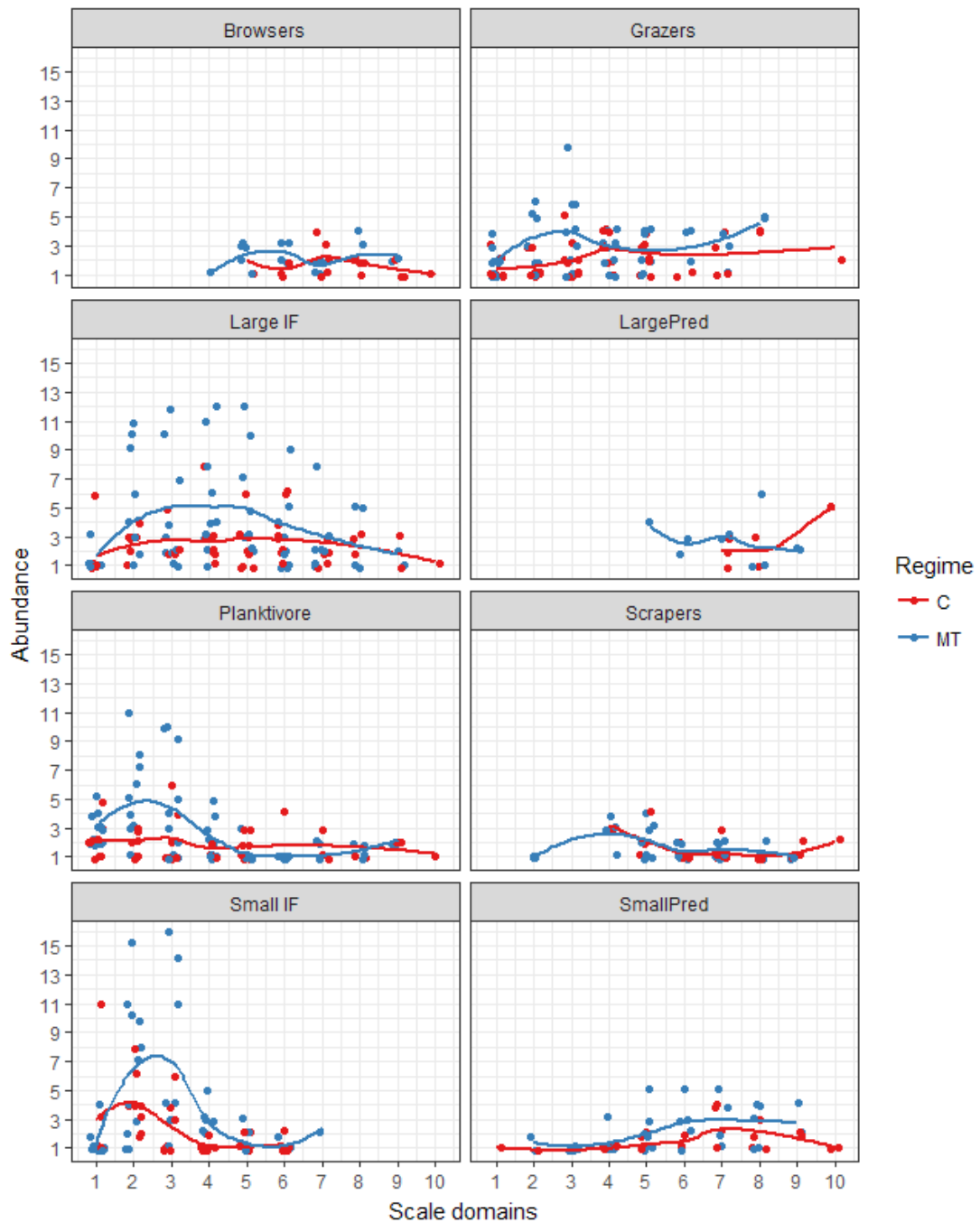


Figure 4.8 Each plot shows the number of species of that functional group sampled at each scale domain. Each community is plotted as an observation, and color indicates whether it is a coral or macro-reef dominated community. Smoothing curves are also colored by regime, and allow a comparison of relative within-scale redundancy for the two regimes for each functional group.

Another possibility derives from a basic premise of the cross-scale model that argues that disturbances that impact the abundance of a species often occur at specific

scale domains within the systems, as opposed to operating in a scale-invariant manner. Fishing, for example, typically targets larger-bodied fish. The cross-scale model presumes that in the event of a scale-specific disturbance, compensatory responses are most likely to occur first by species in that same scale domain that also belong to the same functional group but have a different response diversity, so are not impacted by the disturbance. Functionally redundant and similarly sized species, if they exist, are most able to take advantage of resources at that scale (Ernest & Brown 2001; Elmqvist et al. 2003; Bellwood et al. 2004; Nash et al. 2013a). In other words, they will be competitively released and in the best position to take advantage of the freed-up resources due to the fact that they forage at similar spatial and temporal scales as the species whose abundance was reduced. It is possible, therefore, that the increased redundancy of function at smaller-medium scale domains for macro-turf communities reflects a compensatory response as a result of the loss of larger-sized fish.

Functional group classification

This analysis classified functions in the most simplistic manner possible. Species that in reality represent multiple continuous traits and vary for the ‘amount’ of trait they express across individuals in a population were reduced to one category of a single categorical trait. Petchey (2004) demonstrated that *a priori* construction of functional groups may be no better than randomly assigning species to groups. However, assigning values to reef fish for multiple traits, although desirable, is especially challenging because for many species multi-trait information is unavailable. At the same time, coarse classification methods fail to account for the way in which functional traits in fish with indeterminate growth can change over their

ontology. Using continuous multi-trait data would not only require exhaustive information about variation in trait expression within species, it would also require creating arbitrary cut-offs where fish above or below a certain size change their trait categorization. It has been shown that coarse functional categorizations such as those used here can still adequately discriminate variation between communities (Nash & Graham 2016) but information is inevitably lost. From our perspective, the challenge is to classify species with multiple or continuous traits and also understand these traits within and across scale domains. Although sampling data were available for this analysis that represented individual fish sized to the centimetre, current methods to detect scale domains such as the GRI are inadequate for data where many fish have the same size. An alternative method is to use some form of kernel density estimation to identify modes in the distribution, but then it becomes necessary to determine where a mode begins and ends, as all individuals must fall within a mode. Until methodologies can be developed to objectively identify either discontinuities or modes in individual size distributions, our best alternative is to test the addition of more sophisticated functional diversity measures to the three currently used here.

Conclusion

As with any ecosystem, there are multiple environmental and human-driven variables that can impact community composition, abundance, and resilience. This analysis took a novel approach to a well-studied coral reef ecosystem, and assessed whether the cross-scale resilience of reef fish communities differed by region, island, or regime. Due to the complexity of the underlying differences between and among regions and islands resulting from environmental variables such as sea surface temperature, oceanic productivity, and wave energy or anthropogenic variables such

as protected status, history of fishing pressure, access to markets, and nutrient enrichment , it is difficult to draw strong conclusions. Nonetheless, there was a clear signal that the within-scale redundancy of functions was higher for macro-turf sites, both within an island and between islands. Although it may feel ironic that the resilience was higher in the more degraded reef communities, it is a reminder that resilience is not innately good or bad, but merely a measure of a system's ability to remain in its current state given the disturbances it must cope with. In this light, the resilience of degraded sites across the Hawaiian archipelago is higher than coral-dominated sites, suggesting these sites will persist in this regime unless there are significant changes in external drivers, and that coral sites, as a result of their lesser resilience, may be vulnerable to future regime shifts to macroalgal or turf dominated regimes.

CHAPTER 5 THE ROLE OF ABUNDANCE IN THE CROSS-SCALE RESILIENCE MODEL

Introduction

Long before Darwin's *Origin of Species* (1859), humans have carefully observed the natural world and noted what species are present, and in what numbers (e.g. Aristotle's *History of Animals* circa 4th century BCE). Such basic knowledge remains integral to the most advanced natural science theories of our time. One such theory arises from complex systems science, and argues that the resilience of ecological and other complex systems emerges from a suite of attributes that allow the system to flex, absorb, and adapt to disturbances in a way that promotes the long-term persistence of the system in a recognizable configuration (to remain in a regime, or on an attractor; Holling 1973). One of the core attributes that drives resilience is the distribution of species functional traits within and across the scales of the system, as a resilient distribution balances the tension between diversity and redundancy that is common across evolved systems (Peterson et al. 1998; Hillebrand et al. 2008; Page 2010b). Species perform many ecological functions that contribute to system maintenance and processes; these include nutrient cycling, soil formation, primary production, pollination, and more. Recent research has made it clear that long-term system persistence and stability is strongly dependent on functional diversity, as represented by the functional roles species play (Hooper et al. 2005; Petchey & Gaston 2006; Hillebrand & Matthiessen 2009). Diversity, however, can come at the expense of redundancy, because a high diversity means fewer species overlap in their

functional traits so the loss of any one species can mean a loss of that functionality (Mouillot et al. 2013a, 2014). Redundancy, in the form of multiple species that have a similar functional role, provides critical functional reinforcement over time and space. Resilience emerges in large part from the balance of functional diversity and functional redundancy within and across the scales of ecosystems (Peterson et al. 1998).

This cross-scale distribution of function is captured in the cross-scale resilience model, a model that bridges the gap between the mechanisms governing how individual species self-organize, and the emergence of the ecosystem-level property of resilience (Peterson et al. 1998). The cross-scale resilience model currently accounts for which species are present, the scales at which they operate, and the functional roles species play, but not the numbers in which they are present. Metrics like abundance, biomass, and energetics inform us about how much resource is present, and therefore how much specified function is provided, which is currently missing from the cross-scale resilience model. Incorporating abundance into the cross-scale model is not straightforward, as it is not at all certain what configuration of cross-scale abundance would provide the most relative resilience to disturbances, because compensation processes, when broadly defined, can include negative covariation as a result of competitive release, positive facilitation, and intraspecies behavioural plasticity. Our purpose, therefore, is to detail the ways in which we would expect abundance to be relevant to the cross-scale resilience model based on abundance research that has occurred elsewhere in ecology, and to put forward a series of testable hypotheses that would improve our ability to anticipate and quantify how resilience is generated, and how ecosystems will (or will not) buffer recent non-

stationarity in climate processes and other anthropogenic disturbances (Milly et al. 2008).

Background and research motivation

Holling changed the trajectory of ecology when he proposed that ecological resilience “is a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables (Holling 1973) and contrasted it to engineering resilience, which focuses on “stability near an equilibrium steady state, where resistance to disturbance and speed of return to equilibrium are measured” (Holling 1996). In effect, he proposed a new paradigm for ecosystem dynamics; one which described ecosystems as complex adaptive systems with thresholds, emergent phenomena at larger scales that cannot be predicted from aggregating knowledge at smaller scales and non-equilibrium dynamics with multiple alternative stable states. This perspective was in contrast to prevailing views of ecosystems as having linear, predictable dynamics, and a single fixed equilibrium state. Resilience sensu Holling provides a way to conceptualize, measure, quantify, and manage the vulnerability of complex adaptive systems.

As part of his conceptual model of ecological resilience, Holling and colleagues presented a framework to capture both the cycles of change that occur in ecosystems, and the different spatial and temporal scales at which these cycles operate (Gunderson & Holling 2002). The adaptive cycle represents an idealized portrait of the phases of system development, maturation, collapse, and renewal that reflect internal processes of self-organization and evolution over time. Nested adaptive cycles that operate at different spatial and temporal scales are called a panarchy

(Gunderson & Holling 2002). Systems have different resilience at different stages of the cycle, providing insight into how structure interacts with process to drive system vulnerability. Feedbacks at smaller and faster scales can cascade up a system, as in when fire begins in a stand of trees but spreads through the forest, or can act as a top-down constraint, as in when climatic patterns of moisture constrain where forest can develop. This hierarchical structure of pattern and process playing out at distinct spatial and temporal scales is the ecological theatre upon which individual, population, and community interactions unfold.

The Textural Discontinuity Hypothesis (Holling 1992), hereafter referred to as the discontinuity hypothesis, was developed to test the basic proposition of nested adaptive cycles (Holling pers comm, Garmestani *et al.* 2009)). It states that the key processes that structure ecosystems occur at distinct and limited ranges of spatial and temporal scales, called scale domains, driving the emergence of ecological structure that occurs at distinct and limited spatial and temporal ranges of scale. The species' components of this structure are more likely to persist if they have body masses that allow them to take advantage of the available scale domains of resource opportunity, as body mass is allometric with many life history and behavioural traits (Peters 1983). The transition from one scale domain to another is non-linear, creating discontinuities in both ecological structure and animal body mass distributions. These discontinuities exist where there is either extreme variability in structuring processes or no persistent structuring processes. In short, the scale domains identified by analysing distributions of animal body masses and ecological structure for discontinuities reveal the scales at which adaptive cycles operate (Gunderson & Holling 2002). Discontinuities found in both organism body mass distributions and in ecological structure have since

confirmed these ideas (Thibault et al. 2011; Nash et al. 2014a, 2014b; Raffaelli et al. 2015; Spanbauer et al. 2016), as has work on scaling and body mass in other disciplines (Haskell et al. 2002; Fisher et al. 2011; Hatton et al. 2015).

The cross-scale resilience model (Peterson et al. 1998) bridged resilience theory, the discontinuity hypothesis, and panarchy, and was proposed as a measure to capture four elements that were the essence of Holling's original argument for ecological resilience. These are: 1) ecosystems are spatially and temporally multi-scaled, discontinuous, and hierarchical; 2) ecosystems may have multiple alternative states in which they can exist under the same environmental conditions; 3) resilience is an emergent phenomena, and as such results from the interactions of individuals; and 4) the persistence of relationships, processes and functions is more important than stability or stationarity in either species presence or abundance. The model specifically proposes that ecological resilience emerges from the diversity of overlapping functions within a scale domain, and the redundancy of functions across the scale domains, as this is most likely to buffer system level properties against disturbances that occur at particular scales within the system (Figure 1). Wohllleben (2016), for example, describes the reproductive strategy of Central European deciduous trees that produce large seeds coveted by mice, squirrels, and jays for their high oil and starch content (oaks, chestnuts and beeches). Mice often bury their seed stores at the base of the trunk from which they gathered the seeds or within 10 metres of the tree, while squirrels do so up to 100 metres from the tree, and jays will transport the seeds up to 5 kilometres away. Because the seeds are most successful when growing in the shade of their mature counterparts, this overlapping function by seed dispersers across spatial scales provides resilience to the tree community because

disturbance at one spatial scale leading to the loss of a seed disperser can be compensated for by seed dispersers operating at other scales.

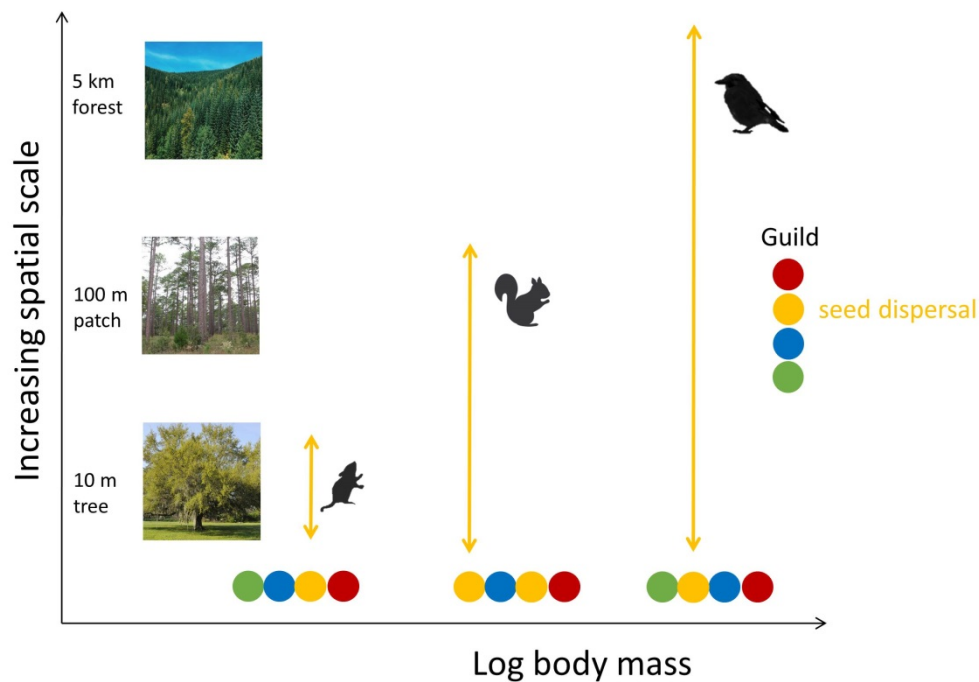


Figure 5.1 Resilience emerges from an overlapping diversity of functions within a body mass aggregation, and a redundancy of functions across body mass aggregations. Species within a body mass aggregation interact with their environment at similar spatial and temporal scales. In this stylized example, seed dispersal is performed by 3 species that operate at distinct spatial scales: a mouse, a squirrel, and a jay. Adapted from (Holling 1992; Wohllleben 2016).

The cross-scale model was seminal because it provided a measure of resilience that captured critical system features that had been somewhat neglected by the traditional ecological literature, and provided a much-needed mechanism to address the provisioning of resilience (Oliver et al. 2015). The model evaluated species presence not in terms of species richness (number of species), but in terms of

the functional composition represented by the community (number of different functions and number of species representing a given function). Functional composition has since been shown to be more critical to the maintenance of system-level features like primary productivity and persistence within a regime than species diversity (Rudolf & Rasmussen 2013; Soliveres et al. 2016). Secondly, the model explicitly incorporated an objective evaluation of the scales at which process and pattern unfold, something long argued by Wiens and others as paramount to any robust understanding of ecosystem dynamics and behavior (O'Neill et al. 1986; Wiens 1989; Levin 1992). However, what is currently missing from the model is an understanding of the importance of the *abundance* of organisms and their functional traits with regard to how they are distributed within and across the scales of an ecosystem. This is an important consideration because if the cross-scale hypothesis is accurate, the resilience of ecosystems is dependent on the distribution of these functional traits within and across scales. As the function is imparted by species that are themselves unevenly distributed across scales and even within scales, what is the effect of fluctuating organism abundance on ecosystem function and thereby resilience?

Furthermore, the cross-scale resilience model has always implicitly assumed that the primary mechanism by which the cross-scale distribution of species' functions copes with disturbance is via changes in the abundance of species within the same functional group as a result of either compensatory dynamics or differential responses to environmental drivers (response diversity), but there have been few tests of this assumption (though see Angeler *et al.* 2013, 2014, 2015). The case for response diversity was put forth in the original cross-scale resilience paper (Peterson

et al. 1998), but validations of its importance have been generic in the sense that they have confirmed that response diversity facilitates the coexistence of species and maintenance of ecosystem properties (Elmqvist et al. 2003; Baskett et al. 2014; Scranton & Vasseur 2016; Wieczynski & Vasseur 2016), as opposed to determining whether the distribution of species with different responses to disturbances within and across system scales is non-random and contributes to or diminishes system resilience (though see Nash *et al.* 2015). Adding response diversity to an assessment of cross-scale resilience is conceptually straightforward but in practice can be difficult due to the lack of necessary species-specific knowledge (Lefcheck et al. 2015). We seek to discuss the ways in which including species' relative abundances into the cross-scale resilience model can clarify and expand our understanding of resilience, as well as how response diversity might impact resilient abundance distributions. Furthermore, we will articulate broad predictions and testable hypotheses pertaining to abundance and the cross-scale resilience model.

Role of abundance in ecosystem resilience and the cross-scale model

According to the cross-scale resilience model, species within a functional group will be distributed non-randomly across the scale domains of a system such that interspecific competition is reduced because species that forage and use ecological resources in a similar way will be separated by the scales at which they do so as they have distinctly different body sizes (Peterson et al. 1998; Greenfield et al. 2016). Niche compartmentalization by size has been demonstrated by several ecological models and theories (Vergnon et al. 2012; Rudolf & Rasmussen 2013; Scheffer et al. 2015). However, this does not explain how abundance among species will be distributed within a functional group or at specific scales. Both phylogeny and

broader abiotic factors constrain the number of scale domains at which a functional group can occur. For example, in a North American dry mixed grassland, aerial insectivores tend to occur at smaller scale domains than do aerial carnivores. The largest aerial insectivore is the Common Nighthawk (*Chordeiles minor*) at 76 g, whereas the largest aerial carnivore is the Golden Eagle (*Aquila chrysaetoes*) at ~ 4 kg (Sundstrom et al. 2012); in other words, not all functions occur within all body size classes.

The ecological literature is rife with research on the spatial distribution of abundance and the role of abundance in ecosystem processes and stability. Some basic tenets have emerged from this body of work, and include the following: there are few common species and many rare (Gaston & Fuller 2007; Connolly et al. 2014); there are more small species than large species (Damuth 1981); species abundances are typically unevenly distributed within their geographic range (Maurer 2009); and species with a high abundance/biomass have large effects on ecosystem processes (Suding et al. 2008; Petchey & Gaston 2009; Stuart-Smith et al. 2013) although rare species can also contribute to the maintenance of such processes (Mouillot et al. 2013a). These tenets shape our expectations for the patterns of abundance and function that we anticipate within the context of the cross-scale resilience model, but also create many new questions.

Abundance distributions

Prior research within the broader ecological literature on patterns between body size, abundance, and functional traits/guilds suggests that abundance distributions within and across scales will be skewed; specifically, the most abundant species will be in different functional groups, and will also have distinctly different

body sizes (Figure 2) (Damuth 1981; Petchey & Gaston 2006; Vergnon et al. 2009; Magurran & Henderson 2012).

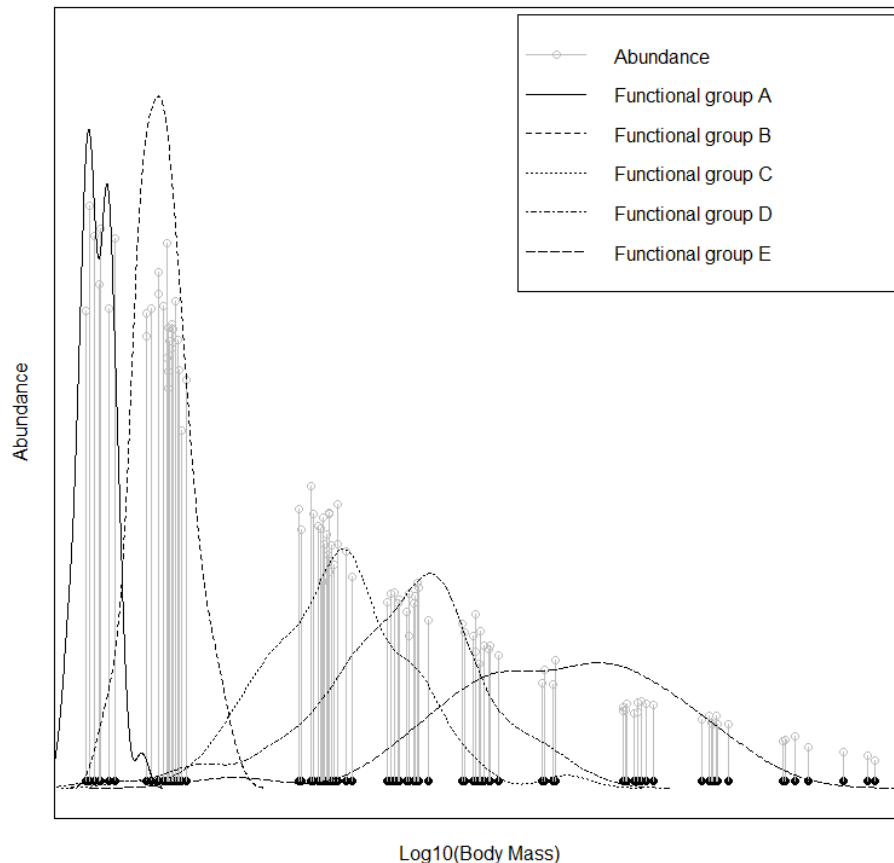


Figure 5.2 Prediction for distribution of abundance within functional groups, and across scale domains. Clusters of similarly-sized species (represented by filled circles on x-axis) interact with their environment at similar spatial and temporal scales, so experience the strongest direct competition. Our expectation is that that the most abundant species will belong to different functional groups, and they will occur at different spatial and temporal scales

Species with similar body sizes use resources at similar spatial and temporal scales, but competition is reduced by utilizing different resources (Rudolf & Rasmussen 2013). Vergnon et al. (2009) found that the most abundant phytoplankton species were far apart in terms of body size (the scale domain at which they operated), suggesting that strong interspecific competition prevents similarly-sized species from

attaining high abundances. Functional diversity within a scale domain is both more diverse than expected by chance, and robust to community change (Forys & Allen 2002; Sundstrom et al. 2012), meaning that species that have a similar size are more diverse in their functions than is expected by chance; even with species turnover, that diversity of function amongst similarly-sized species is retained (Forys & Allen 2002). However, rare species tend to be more vulnerable to extinction due to their small population sizes (Davies *et al.* 2000; Gaston & Fuller 2007; Rohr *et al.* 2016; though see Sundstrom & Allen 2014), which suggests that as a general principle, a more even distribution of abundance across species would reduce extinction risk and increase resilience (Rohr et al. 2016) because the loss of function represented by a loss of a species would be lessened.

However, response diversity may be more relevant than evenness of abundance. Consider a situation where response diversity is high, but abundance is strongly skewed. As long as less abundant species have a differential capacity to cope with a disturbance and can maintain or increase their abundance in response to a disturbance, then they can compensate and provide critical function until the dominant (with regard to abundance) species rebound. If all species who share a similar functional role or operate at similar spatial and temporal scales have the same response to a disturbance, then that functional role or functionality at that particular scale domain will be effectively eliminated unless populations rebound. Therefore, within the context of the cross-scale model, either relative evenness or relative skewness could result in resilient distributions of abundance, depending on the degree of response diversity present in the system. Unfortunately, there is a lack of data on the differing response thresholds of species to disturbances which largely prevents

researchers from incorporating response diversity into general modelling efforts (Lefcheck et al. 2015).

Researchers investigating skewness in abundance have made a strong case that common or dominant species provide the bulk of ecological function, while other researchers have shown that rare species provide unique functions that are also critical, especially as insurance against particular disturbances (Ellingsen et al. 2007; Gaston 2010; Mouillot et al. 2013a; Inger et al. 2015). Claims that high species evenness is a feature of undisturbed natural communities go back to Odum (1969) but were poorly substantiated at the time. More recent theoretical and empirical work argues that dominance versus evenness is a function of how niche space is partitioned; dominance is associated with homogenous and low dimensional resource structure found in disturbed biotas, whereas evenness is associated with more diverse and complex resource structure that is a feature of undisturbed biotas (Sugihara & Bersier 2003; Hurlbert 2004; Rohr et al. 2016). Although the prevalence of strong dominance in real-world communities suggests that the debate is, to a certain extent moot as most real communities are dominated by a few common species (Dangles & Malmqvist 2004; McGill et al. 2007; Connolly et al. 2014; Winfree et al. 2015), changes in the degree of dominance may nevertheless be an important indicator of changing system resilience (O’Gorman et al. 2012).

Given the general patterns in body size, abundance, and functional groups just discussed, our expectation regarding general abundance patterns within and across functional groups and system scale domains is that the most abundant species will belong to different functional groups, and will operate at different spatial and temporal scales (Figure 2) (Walker et al. 1999; Sugihara & Bersier 2003; Vergnon et

al. 2009, 2012; Magurran & Henderson 2012). We also expect that the degree of skewness in both abundance within a functional group, and abundance within a particular scale domain, will differ from system to system based on the innate degree of species and functional richness of the system and the degree of anthropogenic degradation it has experienced—systems with more habitat complexity and higher resilience will have less dominance and more evenness than simple or degraded systems. Testing these patterns across multiple datasets, as well as comparing less degraded and degraded habitats, would be informative. We argue that if degree of dominance (skewness in abundance) reflects, among other things, the complexity (or lack thereof) of niche space, then changes in dominance/evenness will be most relevant to tracking resilience over time, as changes in the degree of dominance reflects changes to the underlying resource template.

Finally, there are two other aspects of abundance to consider: expectations regarding the shape of the distribution of abundance within a scale domain, and the role of variability in abundance as it relates to resilience. Recall that the species within a particular scale domain are similarly-sized. Thus, if we plot their abundance and retain their ranking, we would expect their distribution to be unimodal with the mode in the center of the distribution (Figure 3). This is different than plotting abundance against body size because it conserves their location in the scale domain relative to each other's body mass, as well as their distance from a discontinuity (gap between scale domains as represented by a range of body mass where no species are present).

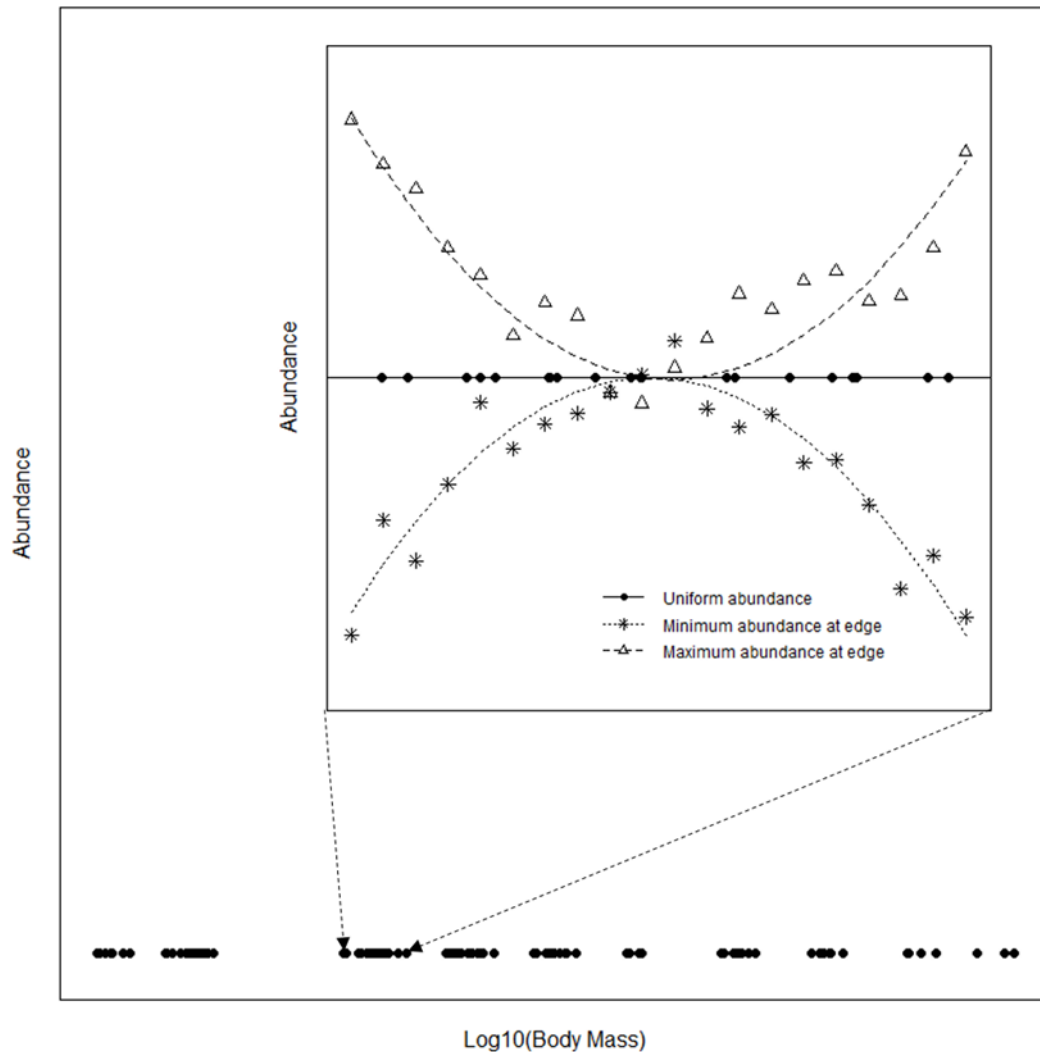


Figure 5.3 Testable hypotheses regarding how species abundances are distributed within one body mass aggregation for a taxa. Clusters of similarly-sized species along the x-axis are represented by filled circles. Clusters are separated by discontinuities where no species fall. Inset graph depicts 3 hypotheses for how abundance within a cluster might be distributed: open triangles depict scenario where maximum abundance occurs in species falling at the edges of the body mass cluster; asterisks depict scenario where maximum abundance occurs in the center of the body mass cluster, and closed circles depict scenario where abundance is uniformly distributed across species in the body mass cluster.

We expect species within a scale domain to have peak abundance in the middle of the distribution because it is thought that resources in the centre of a scale domain are more stable over space and time, whereas the edges or discontinuities are areas of

high spatial and temporal variability (Allen et al. 1999; Allen & Saunders 2002; Sundstrom & Allen 2014). Stable resources should sustain greater abundances relative to resources that are highly variables in space and time. However, it is also possible that there will be higher abundance at the edges of the scale domains, or that abundance will be uniform, although there is less biological basis for either of these possibilities (see Figure 3 for competing hypotheses).

Variability in the spatial and temporal dimensions of resource structure is also associated with variability in abundance, as evidence from the Everglades has shown that species whose body masses place them close to a discontinuity experience higher variability in their abundance than species located near the centre of a scale domain, and this is believed to be related to the increased variability in resources at discontinuities (Wardwell & Allen 2009). Furthermore, others found that within a scale domain, species closer to the discontinuities had lower abundance than species in the center (Vergnon et al. 2012). We predict that variance in abundance of a functional group may be more important over time than total abundance, as variance in abundance is a typical early warning indicator of a regime shift (Carpenter & Brock 2006), and therefore provides clues about changes to the underlying resource template and resilience. If this is the case, then temporal data would be necessary to understand the natural range of variation present in both species abundances and system level provision of functionality.

The role of compensation

Compensation or functional redundancy can occur by a variety of pathways, ranging from classic compensatory dynamics such as density dependence and negative covariation via competitive release, as well as positive facilitation,

differential response diversity, and synchrony, or positive covariance (good times for one is good times for all) (Houlahan et al. 2007; Thrush et al. 2008; Gonzalez & Loreau 2009). There is no consensus in the literature as to the relative prevalence or importance of these different mechanisms, or the degree to which compensation is even likely. Most biodiversity-function models, including the cross-scale resilience model, assume that species in the same functional group will provide functional redundancy in the event that a disturbance reduces abundance of individuals within the functional group. This is strongly supported by the work of Soliveres et al. (2016) which shows that there is little overlap (~ 30%) among different functional groups; in other words, different functional groups provide different services. Work in experimental grassland communities also suggests that compensation is more likely to occur by species in the same functional group (Roscher et al. 2011). Expanding upon this idea, we expect that functional compensation would first occur via species in the same functional group operating at the same scale domain, if there are any, and then by species operating at nearby scale domains, and this compensation would be reflected in either increases in abundance, behavioural plasticity, or both.

Resource utilization is scaled to body size. For example, while a moose and a mouse may forage on similar resources, a mouse may perceive something as a resource that is not discernible to a moose. Species in the same functional group that operate at similar spatial and temporal scales are most likely to provide compensatory functionality. For example, in long-term rodent community data, Ernest et al. (2008) found that when the largest granivore, kangaroo rats, were experimentally removed from plots, smaller species in the same functional group increased in abundance but only utilized 14% of the energy made available. It wasn't until a new species

similarly-sized to the kangaroo rat colonized 18 years later that those resources were once again used at a rate comparable to when the kangaroo rat was present. There are, however, two important limitations with regard to the capacity of a community to show compensation (Kremen 2005; Davies et al. 2012). The first is that the substitutability of species is imperfect, and may be especially limited when quantifying the *amount* of function. It is not clear how to account for the spatial and temporal extent at which a large, but far less abundant species performs its functional roles, as opposed to the much smaller spatial and temporal extent of more abundant species. For example, scraping function (i.e. the removal of algae and opening up bare substratum for coral larval settlement) has a non-linear relationship with body mass in herbivorous coral reef fishes (Lokrantz et al. 2008), so the loss of a larger herbivorous scraper likely has a disproportionate effect on the provision of that function (Nash & Graham 2016).

These are particularly difficult questions to answer when different species are providing the functional compensation and therefore are not only potentially operating at a different scale domain but also have imperfect redundancy in functionality as no species can be an exact replacement for another. Second, species in the same functional group may not be able to provide compensatory function if they are prevented from colonizing due to dispersal limitation or habitat fragmentation (as in the dispersal limitations in the rodent example), or if they have the same response to the disturbance. Given that resilience is often assessed at the ecosystem level, it is reasonable to expect that the reduction in functions resulting from localized extinctions or disturbances within that system may remain uncompensated if other species within that functional group cannot overcome barriers to dispersal. Although

testing data from different systems to assess patterns is necessary, comparing abundance distributions within a functional group between degraded and undegraded habitats would also be valuable.

Despite the limitations on compensation discussed, we also expect that even the small amount ($\sim 30\%$) of overlap in function between functional groups documented by Soliveres et al. (2016) in their assessment of 150 grasslands, would, if typical of other ecosystems, provide a resilient balance between direct competition amongst species operating at the same spatial and temporal scales, and redundancy, or insurance against disturbances, as predicted in the original cross-scale model (Peterson et al. 1998). Both trait overlap and behavioural plasticity could provide secondary compensatory function (Chong-Seng et al. 2014; Nash et al. 2016). Measuring changes in abundance over time would allow us to test whether functional compensation occurred first via species in the same functional group operating at the same scale domain. Compensation occurring from changes in behavior as a result of trait overlap or behavioural plasticity would be more difficult to track, and would require energetics analyses such as Ernest et al. (2008), or foraging behavior studies such as (Nash et al. 2012). Plasticity in foraging behavior may also eventually manifest in morphological change to traits like body size; despite widespread beliefs that body size is conservative there are examples of rapid evolutionary change in body size and other morphological traits (White et al. 2004; Ozgul et al. 2010; Brown & Bomberger Brown 2013).

The importance of response diversity (Elmqvist et al. 2003), positive covariance, and positive facilitation should not be neglected, as they operate independently of competitive release, and may be more important than previously

understood (Bruno et al. 2003; Houlahan et al. 2007; Thrush et al. 2008; Werner et al. 2014). The contradictory evidence in the literature with regard to the relative importance and frequency of competitive release versus positive facilitation, degree of response diversity, or positive covariance suggests that the strength of their roles is likely to differ from one context to another, making generalized predictions difficult. Nonetheless, we predict that a reduction in abundance of one member of a functional group is most likely to be compensated for by a similarly-sized species within the same functional group, regardless of whether it is due to competitive release or response diversity.

Abundance versus biomass and energetics

Discontinuities in body size distributions and ecological structure tell us about the scales at which resources and species are present, and functional classifications inform us about the functional roles species play, but abundance, biomass, and energetics inform us about how much resource is present, or how much function is provided (i.e. area of reef scraped by herbivorous fishes, or amount of carbon stored by soil microorganisms). Selecting which metric to use in a cross-scale assessment may differ according to context and the research question, as White et al. (2007) describe abundance, biomass, and energetics as alternative currencies that do not always show the same pattern. Each metric captures only a piece of the puzzle of resource partitioning. Classifying species by functional roles often resorts to trophic levels and thus indirectly assumes that who eats what is the most critical functional contribution. Similarly, energetics quantifies how much energy an individual or species consumes, but tells us little about the provision of other functions.

Abundance and biomass both speak to amount of function in the sense that either

more individuals or more biomass of individuals will theoretically translate into more function provided. However, abundance does not incorporate differences in how the rate or amount of function provided by an individual scales to body size, a relationship which cannot be assumed to be linear. If the goal is to understand how changes in the distribution of species and the functions they provide within and across scales drives system-level resilience, it may well be that quantifying total functional biomass at scales (i.e. area of reef scraped/ g of herbivorous fish) is more sensible than total functional abundance (area of reef scraped/number of herbivorous fish). However, tracking variance in amount of function provided within a functional group will, in some circumstances, likely require energetics, as functions such as carnivory require understanding the various consumption rates of carnivores of differing sizes.

Biomass in a size class or age class, rather than abundance, is commonly used in aquatic systems (White et al. 2007). Magurran et al. (2012) argue that biomass within functional groups explained processes structuring an estuarine community more clearly than numerical abundance. Biomass may also be meaningful for terrestrial systems when trying to quantify, compare, and weigh functional contribution by differently-sized species operating at different scale domains. However, it is possible that abundance and biomass in terrestrial systems express the same general pattern over time, as robust evidence suggests that these patterns are highly conserved at the scale of ecosystems, even while component populations can vary widely (Ernest & Brown 2001; Hatton et al. 2015). Regardless of which metric is used, we expect that total amount of function provided by a functional group should have non-directional change over time (accumulated changes exhibit no net direction) due to response diversity to environmental drivers (Houlahan et al. 2007; Thrush et al.

2008) and/or compensatory responses (Gonzalez & Loreau 2009). This expectation assumes that the system remains within a regime (basin of attraction), and that all species in a functional group do not have the same response to environmental disturbance (Fischer et al. 2001; Elmqvist et al. 2003). We propose testing this hypothesis with both abundance and biomass. Declining trends in total biomass within a functional group (total functional abundance) would be a predictor of declining resilience as it would indicate a reduced ability to compensate (Gonzalez & Loreau 2009). Directional trends in the total biomass within a scale domain would indicate changes to the underlying resource template, and thus a possible regime shift (Dossena et al. 2012; O’Gorman et al. 2012).

Directional changes that indicate a regime shift versus normal range of variation

Species’ abundances can vary from year to year in response to local, regional, and climate-driven processes. For example, in response to a climate-driven drought event, chorus frogs waxed and waned, transforming from rare and narrowly distributed to abundant and widely distributed, and then back again, due to their species-specific response to the climate disturbance (Werner et al. 2014). Only sufficient temporal data can detangle whether such transitions are indicative of a directional change in chorus frog abundance indicative of fundamental changes to key system processes and the underlying spatial and temporal scales of ecological structure, or if the changes fluctuated within a normal range of variation. Without monitoring data that includes other species within the community, it can also be difficult to assess whether directional changes within one species are compensated by other species, or indicate a directional change to the underlying resource template

indicative of a regime shift. As an example, the long-term rodent community work by White et al. (2004) showed abundance shifting down the body mass axis, moving from larger rodents to smaller rodents. To further complicate things, they found that four of the nine species actually increased in average body size over time. The landscape was transitioning from a grass-dominated regime to a shrub-dominated regime, driving the aforementioned shifts within the rodent community. The scales at which resources were available was shifting, and this was reflected in both intraspecific plasticity (adjusting body size) and a shift in the location of abundance for granivorous rodents along the body size axis.

In a classic freshwater aquatic example, Carpenter et al. (1985) demonstrated how trophic cascades can shift biomass both across trophic levels and along a body mass axis—an increase in piscivore biomass drives reduced planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass. The dynamic shifting of biomass across trophic levels demarcates the changing scales at which resources are available. Furthermore, community composition in a presence/absence sense may not change at all, even while changes in the key processes structuring the system have dramatically changed the amount of biomass at particular trophic levels and spatial and temporal scales. Two highly conservative features of trophic communities, which can be understood as functional groups, are particularly relevant here: Hatton et al. (2015) found that both aquatic and terrestrial trophic communities maintain a near constant size structure, in that the mean body mass for a trophic community (total biomass in community divided by total numerical density, giving mean body mass) is constant for both predator and prey communities. In other words, the carnivore to herbivore body mass ratio is constant, though the biomass ratio fits a

power law, so that as the biomass of prey increases, the biomass of predators increases more slowly. This makes sense in the context of the discontinuity hypothesis and cross-scale resilience model, which propose that body mass is most directly related to the scales at which resources are available, while biomass reflects the amount of resources available. Furthermore, the constancy of the carnivore to herbivore body mass ratio suggests strong compensatory dynamics, as the amount of prey fit the expectations of the body mass ratio despite variable abundances of species within the functional group (Hatton et al. 2015). Given the robustness of this body mass ratio, a directional change in the total amount of biomass may indicate a regime shift, and the scales at which biomass is lost or gained will provide clues about the drivers of that shift. Others have also shown that patterns of abundance over time at the system-level are stable relative to individual population abundances (Ernest & Brown 2001; Ernest et al. 2008). We predict that this general relationship wherein variability within populations is higher than variability in system-level provisioning should hold unless a regime shift is close, in which case variability in system-level function should increase. An impending regime shift should be preceded by either a change in the scales at which abundance and/or biomass are allocated, or a directional change in the overall biomass within a functional group. Discriminating between abundance changes resulting from stochastic disturbance that may be buffered or compensated by other species, and bottom-up changes to the resource template will be critical.

Caveats to incorporating abundance into the cross-scale model

As the old adage goes, the devil is in the details, and the role of abundance in cross-scale resilience seems likely to be as complex as our understanding of

abundance in other ecological relationships. We anticipate that there are likely to be general patterns in the distribution of abundance of functional groups within and across ecological scales, and that directional changes in the system-level provision of function will be an indicator of reduced resilience and an increased vulnerability to a regime shift. However, we recognize that there is much we do not know, and present the following issues as part of an additional research agenda needed to flesh out our understanding of the role of abundance in ecological resilience.

First, systems are neither static nor changing monotonically across all scales. Nested adaptive cycle dynamics ensure that processes that occur at different spatio-temporal scales ought to be in different stages of the adaptive cycle. In other words, processes of development, maturation, collapse and renewal do not occur in synchronicity at all spatial and temporal scales. In fact, asynchrony of such processes is a critical component of resilience, because such modularity prevents disturbances from cascading unchecked up and down system scales. However, we would expect a different distribution of abundance to be resilient depending on the phase of the adaptive cycle under consideration.

Secondly, abundance per se may be less important than species functional richness. For example, we know that rare and seemingly redundant species play a critical role in the long term persistence of system resilience and stability because they are a functional ‘reserve’ that comes into play when disturbances impact key species. Their abundance is less relevant than their presence. The importance of abundance, then, is restricted to species that play a role in key feedback loops or keystone processes, or the few highly common species that provide the majority of function (Gaston 2008, 2010). For example, in the classic spruce-budworm example

(Ludwig et al. 1978), budworms are controlled by insectivorous birds in the young, growing forest. Qualitative analysis indicates that if other factors controlling budworm outbreak were held constant, bird populations would have to be reduced by two-thirds before there would be a qualitative change in budworm-forest dynamics (Holling 1988).

Third, while most of the work to date in this field has focused on terrestrial taxa such as mammals, birds, and reptiles, within which species have relatively differentiated functional roles, it is less clear how to address communities of taxa that perform a similar function, such as phytoplankton. It may be difficult to determine functional role beyond photosynthesis, reducing the ability to carry out some of hypothesis testing discussed throughout this paper. Understanding how phytoplankton are distributed within and across the scales of aquatic ecosystems nonetheless has value as paleoecological data has made it clear that diatom communities change dramatically through time in response to environmental change, and as the basis of aquatic food webs, their resilience is critically important. It will clearly be necessary to thoughtfully consider the context of a cross-scale resilience assessment, and the appropriate knowledge needed to make such an assessment relevant for the taxa under question.

Finally, sampling methods and statistical issues may impede our ability to quantify the impact of abundance for a variety of reasons. Methods that assume stationarity are not appropriate, as we must assume directional changes in abundance resulting from climate change and other anthropogenic impacts that simplify or homogenize ecosystems. Sampling protocols for abundance must be able to track changes in functional abundance over time, but also account for scales within the

system. For example, sampling across the entire system for the abundance of a particular function averages out the body mass aggregations, and only tells us about system-level abundance rather than the cross-scale resilience.

Putting theory into practice

A cross-scale resilience assessment begins with a discontinuity analysis, as a means of objectively identifying the scale domains within a given system and serves as the foundation for understanding how species, and therefore their functional roles and abundance, are distributed within and across system scales. The details of performing a discontinuity analysis are amply documented elsewhere (Peterson et al. 1998; Allen & Holling 2008; Nash et al. 2014a) so will not be detailed here. Typically, discontinuities are identified in rank-ordered data sorted by taxon, so for example, birds have been evaluated separately from mammals. However, Holling (1992) showed that bird and mammal discontinuity patterns are linearly correlated as they utilize resources as a function of their size irrespective of taxonomy, so community analyses are theoretically possible. The next step is to classify species into functional groups that are biologically reasonable given the taxon and system under question, and then to analyse how function is distributed within and across scales. The objective of this paper was to articulate how abundance, as another layer of information about the structure of the system, would be distributed within and across system scales, and how we would expect this to relate to compensatory processes and therefore resilience. Of the hypotheses discussed, we feel the most important can be summed as follows.

Dominance, or degree of skewness

It is well established that abundance is generally skewed, in that there are a few dominant species with high abundance, and many species with low abundance. We expect that abundance will also be skewed both within a functional group (which are often defined as trophic levels) (Figure 2), and within an individual scale domain (Figure 3), and furthermore, that the most abundant species will belong to different functional groups, and will occur at different scale domains (Figure 2). However, others have argued that degree of skewness speaks to the degree to which an ecosystem has been disturbed or disrupted, or homogenized (Odum 1969; Sugihara & Bersier 2003). Regardless of the current degree of skewness in a given system and what it reflects about system heterogeneity/homogeneity, we expect that any persistent directional change to the degree of skewness in the abundance distribution of species within a functional group may be an early warning signal of a regime shift, because such a change will reflect a change to the underlying resource template.

Compensation/Response diversity

Resilience as per the cross-scale resilience model is predicated on the assumption that if there is the loss or reduction in abundance of a dominant species, their functional role will be compensated for other species in that functional group who either experience competitive release, or have a different response diversity than the afflicted dominant species. We expect that in that event, compensation will first occur via species in the same functional group and from the same scale domain (body size class), and then from species operating at nearby scale domains. Furthermore, we know that system-level stability in the provision of a function can be maintained

despite (or because of) substantial variance in the abundance of the individual species comprising a functional group, so we also expect that an increase in the variance in abundance of an entire functional group is likely to be more relevant than the total amount of abundance within a functional group. Increased variance suggests a reduction in compensatory or response diversity processes, and may be an early warning signal of a regime shift.

Conclusion

The creation of the cross-scale resilience model was novel, bold, and elegant. It articulated a simple model with clear testable hypotheses. It is possible to summarize in one sentence the primary conclusion of the model: system level resilience emerges from the overlapping diversity of functions occurring within a scale domain, and the redundancy of functions spread across the scale domains. For the cross-scale resilience model to more realistically capture the role of species in contributing to system-level resilience, it is necessary to understand not just how function is distributed within and across system scales, but how the distribution of the abundance or volume of function within and across scales impacts resilience. Adding abundance to the cross-scale resilience model is more nuanced and may never generate such a simple model without extensive caveats, but we feel that general patterns are likely to emerge given sufficient hypothesis testing.

The stable provision of functionality at the system level arises from the degree of compensatory function, response diversity, and behavioural plasticity contained within the system, all mechanisms that buffer disturbances but are rooted in variability in species abundances over time. Thus, it is likely that it is directional change in system-level function or persistent changes in the scale domains at which

functional biomass is present that is likely to denote changing resilience or a regime shift. We have articulated some of the primary ways in which abundance may affect the emergence of resilience as represented by the functional roles species provide, as well as a set of testable hypotheses with which to test these ideas. We feel that this stream of research will provide a rigorous foundation for the quantitative evaluation of ecological resilience.

CHAPTER 6 DETECTING SPATIAL REGIMES IN ECOSYSTEMS

Introduction

The possibility of multiple regimes for ecosystems is now well documented, and methods to detect temporal regime shifts have received a great deal of attention (Scheffer & Carpenter 2003; Guttal & Jayaprakash 2008; Dakos et al. 2008). Less well developed is the application of these tools to the identification of spatial regimes that reflect the boundary between two types of ecosystems (though see Kéfi and others 2014). Spatial data has unique challenges in that while it is not necessary for data points to be equally spaced (Dai et al. 2013; Cline et al. 2014), sufficient spatial sampling resolution is needed to distinguish one spatial regime from another. The identification of spatial regimes is increasingly important due to habitat fragmentation, which increases the proportion of boundaries in landscapes (Kent et al. 2006), and anthropogenic climate change, which is expected to shift ecological boundaries. Studies have already shown rapid altitudinal shifts in montane ecological boundaries in response to climate change (Allen & Breshears 1998; Beckage et al. 2008). Similarly, climate-driven boundary shifts are being detected in marine systems as both spatial shifts in primary production and in individual species ranges, as well as in phenological shifts and changes in community composition (Beaugrand et al. 2002; Edwards & Richardson 2004; Grebmeier et al. 2006). Because ecological boundaries in terrestrial systems typically demarcate the distribution of vegetation and ecosystem type, they provide critical information about the extent and rate of the biological

processes shaping the boundary and driving the maintenance of the regime within the boundary (Yarrow & Salthe 2008). This has implications for both environmental management and biological conservation (Kent et al. 2006).

Boundary identification has been an active area of research in terrestrial ecology and biogeography, and is generally both data intensive and statistically challenging, particularly when it involves vegetation sampling (Kent et al. 2006). The use of remotely-sensed data is less laborious than field work, but the method is poor at distinguishing between physically similar but floristically different vegetation; hence, it may require labor-intensive ground-truthing to verify ecological transitions in plant assemblages (Kent et al. 2006). Boundary detection is further complicated by the multiplicity of scales at which different processes and physical patterns are expressed (Fagan et al. 2003; Strayer et al. 2003), and that the relationship between abiotic variables such as climate, and biotic variables such as vegetation, is often non-linear across boundaries (Danz et al. 2012). Typically, terrestrial ecological boundaries defined for ecoregion maps such as those used by U.S. federal agencies are based on potential plant communities, which in turn reflect differences in bedrock, soil, altitude, temperature, and moisture (Bailey 1983; Omernik 1987). Terrestrial plant communities may not respond as rapidly as animal communities to direct anthropogenic change and climate change (Pearson 2006; Pearman et al. 2008), therefore defining the boundaries between animal communities may better represent current biotic and abiotic conditions. Variation in animal population dynamics provides information on the stability of ecosystem mechanisms, processes, and linkages, and may serve as an early warning signal of shifting regimes (Cline et al. 2014).

Pelagic marine ecological boundaries are typically defined by primary production characteristics (Longhurst 1998) which reflect aquatic properties such as currents, temperature, salinity, nutrients, and bathymetry, but are complicated by the ephemeral nature of features such as oceanographic fronts. Landforms, such as straights, may create another form of boundary between biological communities. Advection across fronts or through physical constrictions between water masses can serve as a driver of both physical and ecological homogeneity, though the degree of connectivity can vary rapidly in space and time (Wassmann et al. 2015). There is much current discussion of appropriate variables by which to track marine ecological change (Rice & Rochet 2005; Samhuri et al. 2009; Rombouts et al. 2013). *A priori*, it is difficult to know which individual taxa or processes represent a spatial regime and thus ecological boundaries. Because of the central role played by zooplankton as a prey item and a grazer, zooplankton data have commonly been used (Hooff & Peterson 2006; Pace et al. 2013), although Scheffer et al. (2003) warn that zooplankton community composition and abundance may be too chaotic to be useful for regime shift prediction except at very high level aggregate states.

Ideally, a monitoring program should be able to forecast far-reaching change such as a regime shift. However, too often monitoring focuses on particular species of interest, effectively barring community-level or ecosystem-level analyses. We use spatially explicit avian and zooplankton community species composition data to test for the identification and location of spatial regimes using Fisher information, an information-theory method with no strict data requirements that is a powerful tool for understanding system-level change within a location, or over space.

Regime shifts and Fisher information

There is widespread acceptance in the scientific community that some ecosystems exhibit multiple regimes, and that the transition between regimes can be abrupt and discontinuous (though see Fukami & Nakajima, 2011; Hastings & Wysham, 2010). Statistical indicators of regime shifts that can act as an early warning signal are thought to represent generic properties that behave in similar and predictable ways across system types (Dakos et al. 2011), and are proposed to have the added advantage that detailed mechanistic knowledge is not necessary for their use. The indicators include critical slowing down, which can manifest as slower recovery rates from perturbation, increased autocorrelation, and increased variance (Scheffer et al. 2009); changing skewness (Guttal & Jayaprakash 2008); conditional heteroscedasticity (Seekell et al. 2011), and the variance index (Brock & Carpenter 2006).

These indicators have transformed our ability to identify variables that change in response to exogenous or endogenous drivers and signal an impending regime shift. However, much remains uncertain. For example, although the various indicators have been tested on model systems and historical data sets with known temporal regime shifts (Lindegren et al. 2012), their performance is not consistent (Seekell et al. 2011; Perretti & Munch 2012; Dakos et al. 2013; Batt et al. 2013) and their ability to predict future regime shifts is unknown (Boulton et al. 2014). Some methods, such as conditional heteroscedasticity, require large, high resolution samples (Seekell et al. 2011) and their applicability to complex systems with multivariate data is questionable because most studies have been conducted using either simulated data or very simple systems (Scheffer et al. 2009; Drake & Griffen 2010; Dakos et al. 2012;

Dai et al. 2012). When models have incorporated realistic levels of ecological noise, the indicators tend to perform poorly (Perretti & Munch 2012). A difficulty in developing early warning indicators is that the critical variables driving system transitions are typically unknown. Brock and Carpenter (2012) cite this lack of knowledge as a “fundamental problem” in leading indicators research.

Researchers have urged that multiple ecosystem variables should be evaluated when interpreting indicators for real systems (Carpenter et al. 2009; Lindegren et al. 2012). For example, Litzow et al. (2013) found that when analysing rising variance in catch data from fisheries, trends in individual fisheries largely failed to be statistically significant, while pooling multiple populations increased their ability to detect a collapse. The variance index (VI) was developed to capture dominant variance trends in multivariate systems (Brock & Carpenter 2006). VI should spike prior to a transition, but results from this index are sometimes unclear (Eason et al. 2014).

Fisher information may address some of the issues listed above. Fisher information is an information theory approach (Fisher 1922) that captures patterns in system dynamics as evidenced by the trends in variables that characterize the system's condition. The approach collapses the behavior of multiple variables into an index that can be used to track changes in dynamic order, including regimes and regime shifts. Historical applications of information theory-based approaches include assessing ecosystem functioning, stability, complexity, and diversity (Anand & Orloci 2000; Svirezhev 2000; Patricio et al. 2004; Fath & Cabezas 2004). More recently, Fisher information has been employed for sustainable environmental management at various spatial scales (Karunanithi et al. 2011; Eason & Garmestani 2012) and to

examine temporal patterns in both terrestrial (Mayer et al., 2007; Eason and Cabezas, 2012;) and aquatic systems (Mantua 2004; Spanbauer et al. 2014; Eason et al. 2016).

While other methods like time series analysis requires a sufficient resolution of data to separate noise from a genuine signal of an impending regime shift, the data requirements for Fisher information are more lenient. A strength of Fisher information is that it can readily incorporate a wide variety of data types and variables and has been used to identify regime changes in various types of systems with data resolutions from relatively small and moderate (Eason & Cabezas 2012) to quite large (Spanbauer et al. 2014). Furthermore, there is no minimum or maximum number of variables needed to compute the index. When assessing a complex system characterized by multiple variables, methods like Spearman rank order correlation have been used in conjunction with Fisher information to determine which variables or groups of variables are critical for shaping the Fisher information signal (Eason & Cabezas 2012). Accordingly, one of the key limitations of traditional statistical indicators is avoided because there is no need to make assumptions about which variables best act as indicators of an impending regime shift, particularly when much is uncertain and our knowledge is limited.

Purpose

Our goal is to identify spatial regimes in avian and zooplankton community data using Fisher information, and compare the extent to which Fisher-identified regime boundaries are coincident with our *a priori* understanding of where these ecological boundaries exist, as per classification systems such as Bailey's (1983) and Omernik's (1987) for terrestrial systems, and marine domain descriptions found in Carmack et al. (2010) and Archambault et al. (2010). The terrestrial ecoregion maps

rely heavily on *potential* natural vegetation based on underlying geological and climatic variables, so significant discrepancies between actual land use, actual vegetative cover, and potential vegetation can exist, and should be reflected in the composition of the animal community. Boundaries in marine systems are not as spatially constrained as in terrestrial systems and the key habitat determinants of species' distributions and community structure are not as easily defined. It is important to note that we are not trying to identify regime shifts that represent a critical transition (e.g. Scheffer 2009), but rather the geospatial point or region at which one ecosystem type transitions into another.

Although Fisher information is suited to multivariate data encompassing a wide range of biotic and abiotic data that characterize any given regime, we used a single taxon dataset from each system (birds and zooplankton). Limiting the data in this way had the benefit of making this a conservative test of the performance of Fisher information that reflects the data readily available to others working on similar problems. We compared the Fisher information results with a range of early warning indicators (critical slowing down, captured by the lag-1 autocorrelation coefficient; variance; kurtosis; skewness; and the variance index), and multivariate methods commonly employed by community ecologists (nMDS (Oksanen 2013), and cluster analysis).

Methods

Terrestrial data

We used USGS Breeding Bird Survey data (BBS) from 30 survey routes along a ~ 1900 km transect. Each BBS route is 41 km long and has 50 stop points located at

800 m intervals; at each stop point, a 3-minute point count of sighted and heard birds is recorded, and data from each stop point are totalled for the route (Sauer et al. 2014). The routes begin in the Rocky Mountains, move due east through the central prairie region, and then veer north into Minnesota, terminating at the western border of Lake Superior (Figure 1). The species abundance data are a snapshot of the 2007 bird community at each route location. The routes are located in 5 Omernik Level III ecoregions (Omernik 1987), but were selected such that there were roughly an equal number of routes in four gross ecosystem types: 8 routes from the Southern Rockies (montane forest), 7 from the High Plains (grassland), 3 from the Central Great Plains and 4 from the Western Cornbelt Plains (total of 7 routes from grassland-agriculture matrix), and 8 from the Northern Lakes and Forest ecoregion (northern forest-wetland matrix). The unequal number of routes among ecosystems was due to data availability; not all routes are covered in all years, as route coverage relies on volunteers. Although we used the Omernik ecoregions as an underlying map layer when selecting routes, there are multiple ecoregion maps used by U.S. land agencies, with sometimes substantial differences between them. None are ‘right’ per se, but all are best approximations of potential vegetation based on areas with similar geology, physiography, vegetation, climate, soils, land use, wildlife, water quality, and hydrology (United States Department of the Interior). We downloaded the complete species abundance list for each route (Sauer et al. 2014) and used it to create a route-species abundance matrix, where abundance is the number of individual birds for each species at each route, with values ranging from 0 – 293.

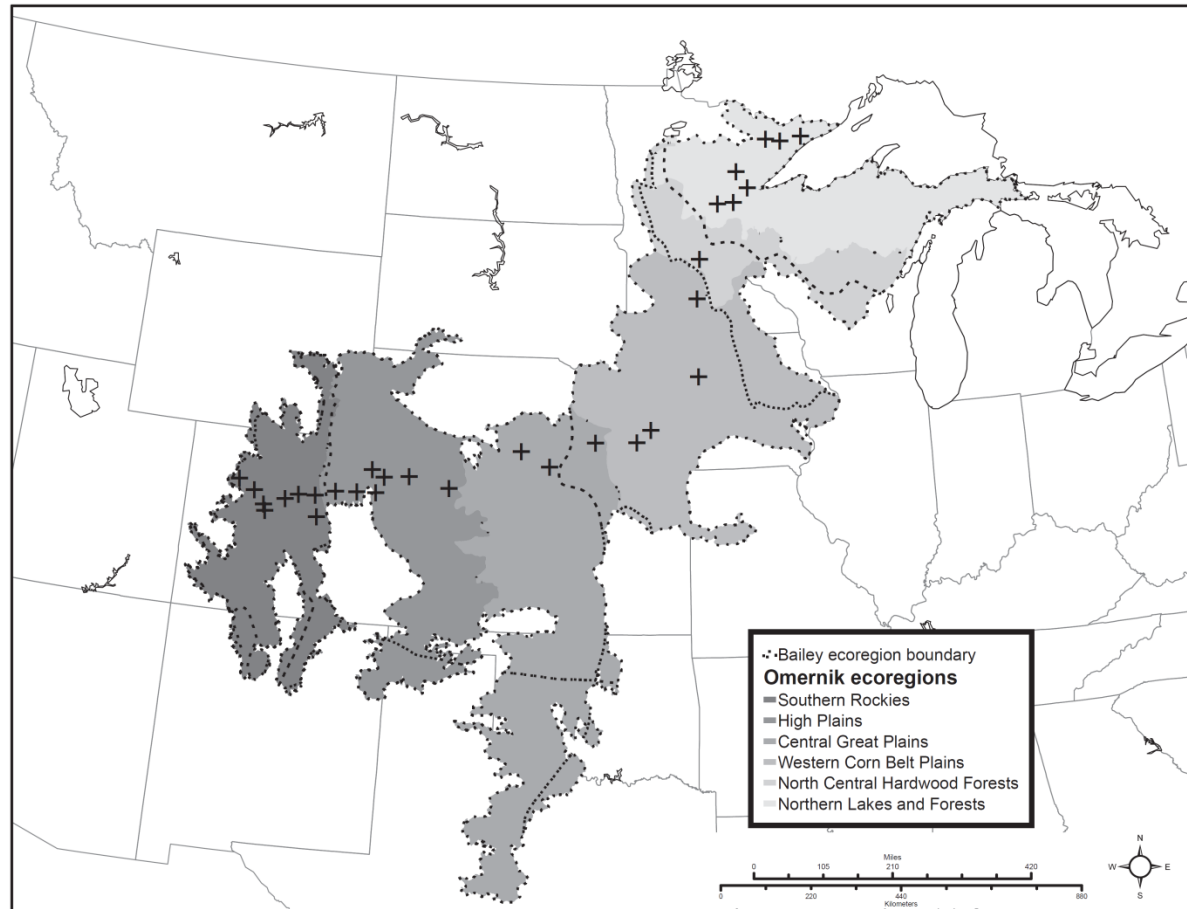


Figure 6.1 The USGS Breeding Bird Survey route locations in the central and northern United States. The Omernik Level III ecoregion boundaries are colored in grayscale, while the Bailey Level III ecoregion boundaries are shown using dotted lines. ([Figure 6.1.pdf](#), 377 KB)

Sampling biases are an issue with BBS data, resulting primarily from under detection of wary, rare, and aquatic species, as well as differences between observers. However, those biases are present across all routes and should not impact the very coarse pattern extracted from the absence/abundance data. Remotely-sensed data for land cover type is also available for a 400 m buffer around each route (Sauer et al. 2014). The land cover data provides a sense of the heterogeneity of the habitat type for each ecoregion. We averaged the percent of each land cover type across all routes for each of the five Omernik ecoregions.

Marine data

Zooplankton community surveys were conducted in 2008, and samples analysed under the auspices of the International Polar Year program, Canada's Three Oceans project (Carmack et al. 2008). The survey traverses 12,000 km from coastal British Columbia just north of Vancouver Island to the Labrador Sea on the eastern side of Canada, crossing through 6 oceanic domains: the Gulf of Alaska, the Bering Sea, the Chukchi Sea, the Beaufort Sea Shelf, the Canadian Arctic Archipelago, and terminates in the Davis Strait/Labrador Sea (Figure 2). Although these oceanic domains share some zooplankton species, they are known to be distinct from each other to varying degrees (Archambault et al. 2010; Pomerleau et al. 2011, 2014). There were 44 sampling locations irregularly spaced along the transect.

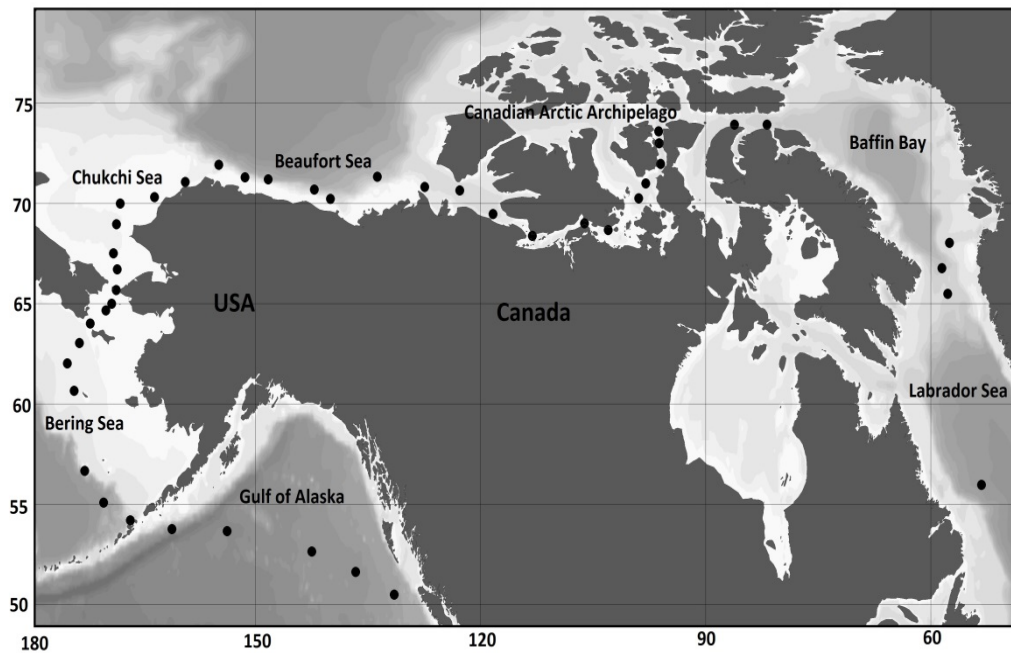


Figure 6.2 Zooplankton data collection locations.

Mixed zooplankton samples were collected from August to September by vertical net hauls with a 236 micron net (typically to 100 m or 7 metres above the bottom), and were preserved in 95% ethanol and 10% buffered formalin. The zooplankton samples were keyed out to the lowest possible taxonomic unit and enumerated and 4th root transformed, as is standard for marine zooplankton data. When possible, the developmental stages of each taxa was counted separately. A site-taxa abundance matrix was created. Sites were ordered from western-most to eastern-most station.

Statistical Methods

Fisher information was developed by Fisher (1922) as a measure of the amount of information about a particular parameter (or system characteristic) that can

be obtained by observation. The form of Fisher information used in this work is based on the probability of observing various conditions ($p(s)$) of the system (Fath et al. 2003; Mayer et al. 2007).

$$I = \int \frac{ds}{p(s)} \left[\frac{dp(s)}{ds} \right]^2$$

This is appropriate for our study because we are interested in determining patterns of change in the condition (or state: s) of a system. From this equation, note that Fisher information is proportional to the change in the probability of observing a system state ($dp(s)$) over the change in state ds (i.e. $I \propto \frac{dp(s)}{ds}$). The significance of this proportionality may be examined using two cases. The first example is a system in which the overall condition does not change from one observation to the next. While such a system may fluctuate within a basin of attraction, it is considered stable because the overall conditions are predictable and the patterns are evident; accordingly, the probability of observing a particular state of the system is high and Fisher information tends toward infinity. The exact opposite is true of a system that is constantly changing. In this case, the system displays no bias toward a particular condition and there are no distinct patterns useful for characterizing the way the system behaves; hence, there is equal probability of the system functioning in any state and Fisher information is zero (Pawlowski & Cabezas 2008).

Karunanithi et al (2008) adapted Equation 1 to handle empirical data from real systems. Through a series of derivation steps, Fisher information (henceforth denoted as FI) is numerically estimated as:

$$FI = 4 \sum_{s=1}^n [q_s - q_{s+1}]^2$$

where $p(s)$ is replaced by its amplitude ($q^2(s) \equiv p(s)$) to reduce calculation errors from very small $p(s)$. Further details on the derivation and calculation may be found in (Mayer et al. 2007; Karunanithi et al. 2008; Cabezas & Eason 2010).

Fisher information has traditionally been used to explore temporal patterns, however, the method can be applied to examine spatial dynamics. The core of the FI approach is to assess patterns in data based on tracking systematic changes in line with some ordering principle such that trends are evaluated over a series of points (e.g., point a, point b, etc.). This sequence may be defined temporally or spatially. The key distinction is that rather than using time as the basis for assessing changes, spatial location is the ordering principle. The basic algorithm for computing FI is as follows: (1) select variables (e.g. x_i , $i = 1 : n$ variables) that characterize the condition of the system (in this case various animal species) and gather data (i.e., species abundance) from each sampling location (l_j) across the route: $(x_i(l_j))$, $j = 1 : m$ sampling locations), such that the abundance of each species at each site defines one point (e.g.. $pt_1(l_1): [x_1(l_1), x_2(l_1), x_3(l_1), \dots, x_n(l_1)]$); (2) assemble the data into a $m \times n$ matrix and divide it into a sequence of overlapping windows that advances one route location per iteration; (3) determine the measurement uncertainty for each variable (UX_i) and use this to define a boundary (tolerance) around each system state. If the measurement uncertainty is unknown then the variation in a stable portion of data may be used as a proxy. This boundary (size of states) defines how much a measurement can vary within a particular state; (4) Use the size of states to determine which points are similar (dimensions stay within the boundary defining a minimum range of variation) and group (bin) similar points together into discrete states; (5) Compute $p(s)$ by counting the number of points binned in each state and dividing this

value by the total number of points in the window; (6) compute $q(s)$ and calculate FI using Equation 2. This process is repeated for each window. Based on empirical assessments, a $h_{win} \geq 8$ was suggested (Cabezas & Eason 2010), however, it is generally set based on the amount of data available. Increasing the h_{win} tends to decrease the magnitude of the FI result and number of FI points, but the basic trends remain intact (Cabezas & Eason 2010).

Different system regimes are controlled by fundamentally distinct processes and exhibit unique patterns. Tracking FI affords the ability to assess changes in these patterns. Regimes are identified as periods over time or across space in which FI is non-zero and the values are relatively stable (i.e., $dFI/dl \approx 0$). While steadily increasing FI indicates rising dynamic order, less change and possible movement to more consistent patterns, declining FI signifies unstable dynamics, loss of resilience and may provide warning of an impending shift (Eason et al. 2014). Although FI typically declines prior to a regime shift (Mayer et al. 2007; Eason & Cabezas 2012; Eason et al. 2014), researchers examined model dynamics to study the behavior of FI in the neighbourhood of a tipping point and found that the behavior of FI depends heavily on the trends in the variables as the system approaches a shift (Eason et al. 2014; Gonzalez-Mejia et al. 2015). It is therefore possible for FI to increase as a system transitions from one regime to another. Such a result is in line with Seekell et al. (2011, 2012), who found both increasing and decreasing trends in early warning indicators prior to a shift.

Once a shift has been identified, the underlying variables can be explored to determine (or compare) the condition of the system in its new state (Eason & Garmestani 2012). Although higher FI values are generally associated with a greater

degree of dynamic order, the level of dynamic order is not as important as the ability of the system to remain stable within a desirable regime. When interpreting FI, a regime is denoted by a relatively stable FI trend (i.e., $dFI/dl \approx 0$) with a high mean ($\uparrow \mu FI$) and low standard deviation in FI ($\downarrow \sigma FI$) or low coefficient of variation in FI ($\downarrow cvFI = \frac{\sigma FI}{\mu FI}$) (Gonzalez-Mejia 2011; Eason & Garmestani 2012). Transitions are identified as periods outside of stable regimes characterized by relatively high σFI and $cvFI$.

The traditional temporal early warning indicators (variance, skewness, and kurtosis) were computed using standard functions. The spatial variants (Moran's I spatial autocorrelation and spatial variance and skewness) were not used because the sequential one-dimensional ordering of the sampling stations lent itself to a space-for-time substitution. Since critical slowing down can be understood as increases in short-term autocorrelation, the lag-1 autocorrelation coefficient was used as an estimate (Dakos et al. 2008). The VI was computed as the maximum eigenvalue of the covariance matrix from the dataset (Brock & Carpenter 2006). Note that the VI and traditional indicators are expected to spike or increase prior to a regime shift, while FI tends to decline (Eason et al. 2014). Fisher information and the traditional indicators were computed in MATLAB (v. 2014b) using a 5 station moving window that advanced one station at a time, where a station was either a BBS route or a plankton sampling site. A window size of 5 ensured that there were FI results for each ecoregion for both studies; using smaller or larger windows resulted in similar trends in the FI results, similar to other studies (Cabezas & Eason 2010). Multivariate analyses were conducted using metaMDS and ordicluster from package 'vegan' (R Development Core Team 2016). The distance matrices for the nMDS were created using Bray-Curtis, and multiple dimensions were plotted in a scree diagram to find the

lowest dimensionality with an adequate ordination fit as expressed by a stress value (<0.2 , (Clarke 1993)). The mean, standard deviation, and the coefficient of variation (CV) in FI were calculated for each regime to explore regime stability.

Results

Terrestrial data

Fisher information detected four regimes and two transition zones which are roughly congruent with *a priori* expectations based on ecoregion maps, but diverge in significant ways (Figure 3). The total drop in FI between the high point in regime 1 and the low point in transition 1 is greater than that between regime 2 and regime 3 (ΔFI of 2.05 and 0.98, respectively), suggesting that the difference in FI between the Southern Rocky Mountains and the 3 Plains ecoregions is greater than the difference among the Plains regions, which is to be expected. Likewise, the total drop in FI between regime 3 (all Plains routes) and regime 4 (Northern Lakes and Forest) is the largest of all (ΔFI of 2.51), indicating that the greatest variation in bird community structure exists between these two regimes.

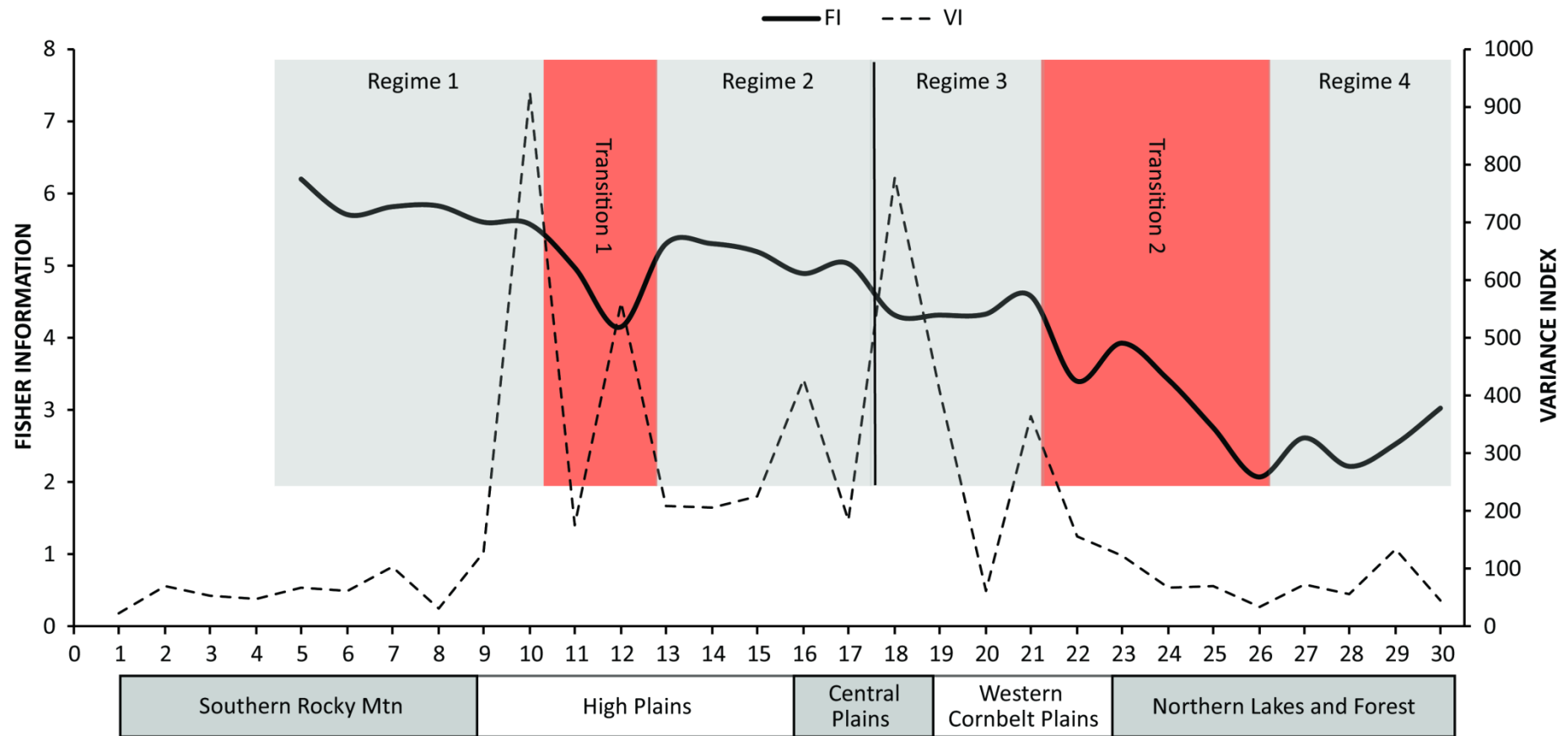


Figure 6.3 Fisher information ((FI; bold solid line)) and Variance Index (VI; faint dotted line) for Breeding Bird Survey community data from 30 routes ordered from west to east along the x-axis. Regimes identified by FI are shown as shaded boxes around the plotted line. The Omernik ecoregion domains under the x-axis allow comparison as to how well the regimes align with the ecoregions, which represent potential rather than actual vegetation. Because one FI value is produced per window, the first FI value is at route 5.

The declining trend in FI from west to east means avian community structure is losing order, which aligns with the reality of increasing intensive agricultural land use. FI classified the community structure in the first High Plains route as being similar enough to the eastern Southern Rocky Mountains to include it in the first regime. There followed a steady loss of order, as reflected in the FI value, across the western High Plains. When FI did stabilize, indicating a new regime, that regime captured routes from both the eastern High Plains and western Central Plains ecoregions, indicating a blurring of the distinction between the two Plains ecoregions in terms of vegetative cover and avian community structure. Similarly, the third regime incorporates routes from the eastern Central Plains and most of the Western Cornbelt Plains ecoregions, indicating that avian community structure did not significantly differ between the two Plains ecoregions. This is not an unexpected result, given that those two ecoregions are, in reality, a grassland-agriculture matrix.

The traditional indicators did not provide clear results and yielded graphs with no interpretable pattern (Figure 4), however, VI provided results that were complementary to FI (Figure 3). The VI peaks in several places which are congruent with regime shifts identified by FI (routes 10, 18, and 21). In general, the VI provides complementary information that supports the trend captured by FI, but is significantly more difficult to interpret when evaluated alone because it is not possible to ascertain whether a peak marks the beginning or end of a stable regime or of a transition zone.

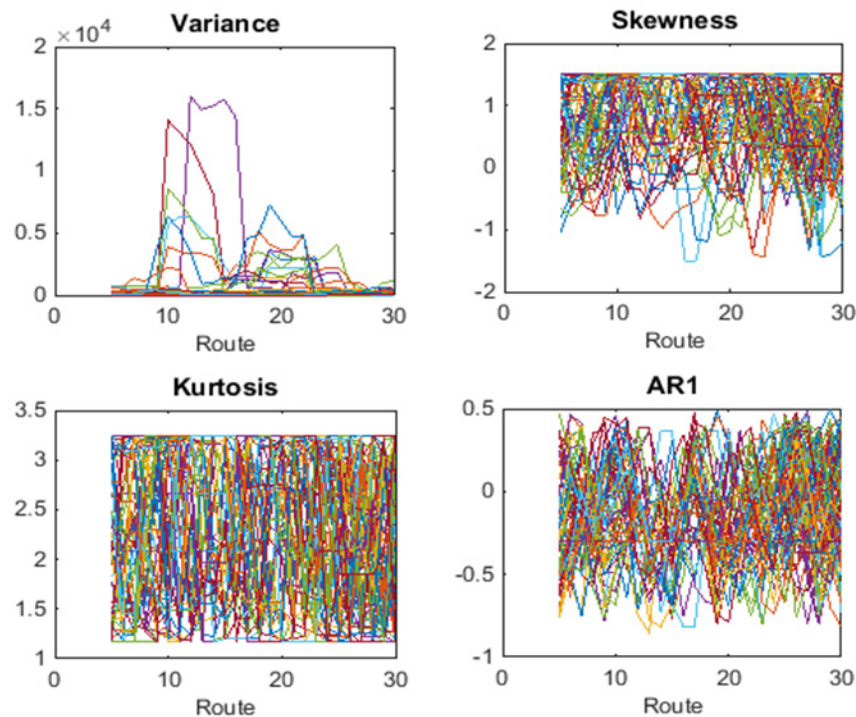
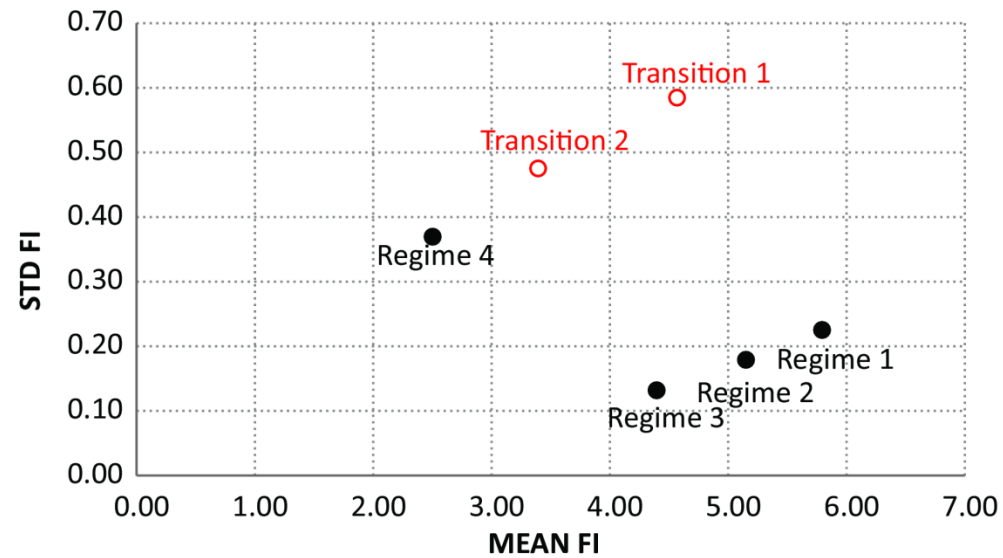


Figure 6.4 Results for traditional regime shift parameters applied to the BBS avian community data: variance, skewness, kurtosis, and ARI (critical slowing down). The graphs are largely uninterpretable when used on multivariate data such as this.

While all three descriptive statistics (mean (μ FI), standard deviation (σ FI), and coefficient of variation (cvFI) in FI) indicate relative stability in each of the first three regimes, the fourth regime, wholly comprised of routes from the Northern Lakes and Forest region, has a lower mean, higher standard deviation, and higher coefficient of variation in FI than the other regions, indicating that there is greater variation in community structure within this ecoregion (Figure 5). Furthermore, the two transition zones have a higher CV than the regimes (except the 4th regime), indicating zones of high variability as community structure transitions from one regime to another.



	Route	μ FI	σ FI	cvFI
Regime 1	5-10	5.79	0.23	0.04
Transition 1	11-12	4.57	0.58	0.13
Regime 2	13-17	5.15	0.18	0.03
Regime 3	18-21	4.40	0.13	0.03
Transition 2	22-25	3.40	0.48	0.14
Regime 4	26-30	2.50	0.37	0.15

Figure 6.5 The stability of each terrestrial regime over space, as defined by the mean (μ FI), standard deviation (σ FI), and coefficient of variation (cvFI) of FI. While regimes 1-3 are clustered together and relatively stable with high μ FI, low σ FI and cvFI, Regime 4 was highly variable (low μ FI, high σ FI and cvFI). The transition periods exhibited the least amount of stability.

The results of the multivariate analyses suggest that while the nMDS (stress value of 0.080 for 2 dimensions) and cluster analysis (not shown on Figure 6 because results are identical to the nMDS) identifies distinct communities that align with the *a priori* expectations of the Omernick ecoregions, they do not distinguish between the High Plains and Central Plains communities. The nMDS (Figure 6) shows the dissimilarity in community structure in terms of the relative position of each route to every other in ordination space, as well as how those routes align with ecoregion expectations by drawing polygons that connect the routes belonging to each Omernick-defined ecoregion. The routes from the three Plains ecoregions are closer to each other in ordination space than either the Southern Rockies or Northern Lakes and Forest routes, indicating that they are more similar in community structure. The first route of the Northern Lakes and Forest region, indicated by FI as part of a long transition zone between regimes, is also very proximate in ordination space to the Cornbelt Plains routes, reflecting their closeness in geographic space. However, the High Plains and Central Plains overlap each, indicating that the nMDS does not perceive them as dissimilar.

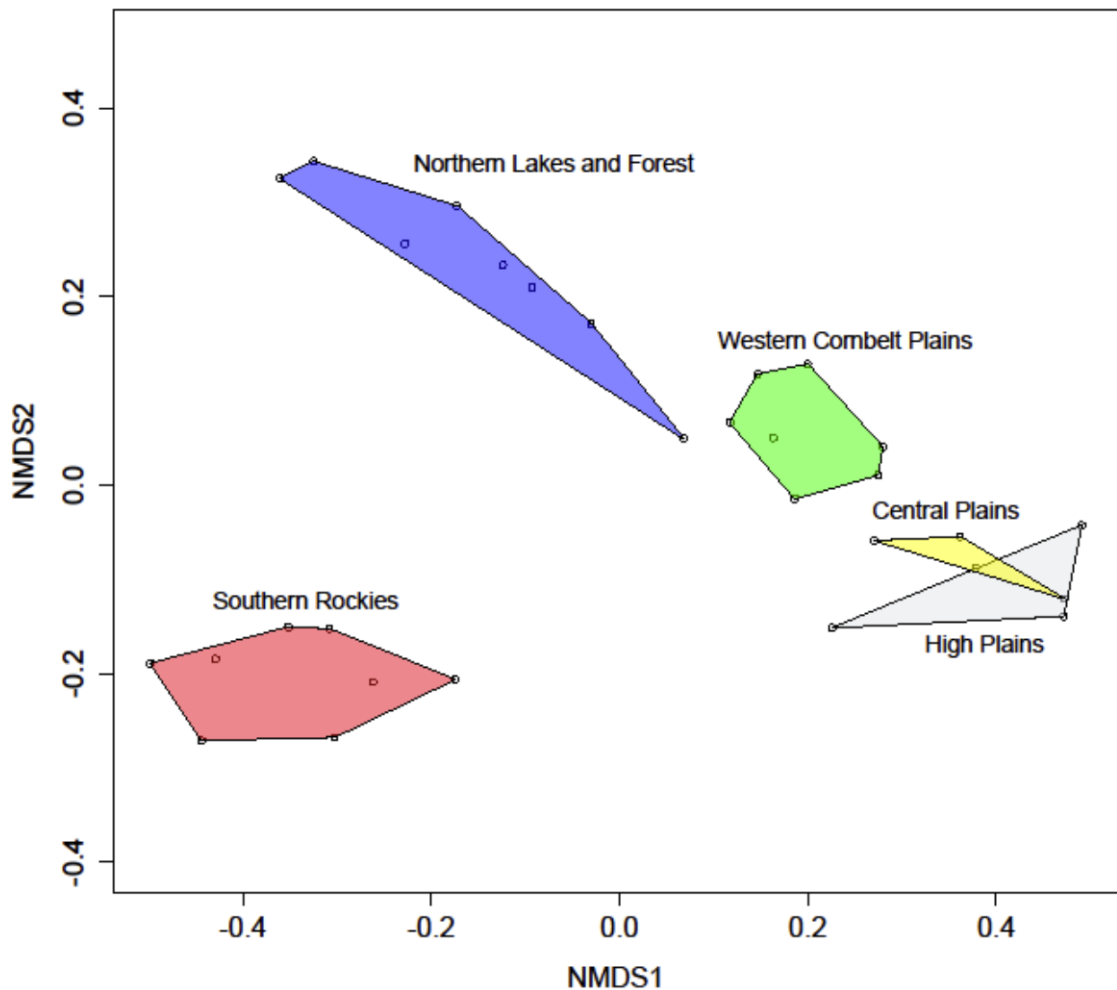


Figure 6.6 Ordination plot for the BBS avian community data ($k = 2$, stress = 0.080). The BBS routes are shown with open circles, while the polygons contain all the routes that fall into the ecoregions (Omernik 1987). The overlap between the High Plains and the Central Plains suggests that these two ecoregions do not substantially differ in avian community structure. ([Figure 6.6.pdf](#), 18KB)

Marine data

Fisher information detected two regimes and two transition zones, which partially align with the *a priori* expectations for the locations of the oceanic domains (Figure 7). FI is low and rises steadily throughout two-thirds of the Bering Sea

domain. Since FI never stabilizes in this domain, much of the Bering Sea is classified as a transition zone. The first regime extends from the northern Bering Sea through the Chukchi Sea. As the transect enters the Beaufort Sea, FI climbs steeply without stabilizing, indicating increasing dynamic order in community structure and classifying the Beaufort Sea as a second transition zone. The second regime extends from the more geographically closed-in waters of the Canadian Arctic Archipelago through the sixth oceanic domain, the Davis Strait/Labrador Sea. The entire distance from the western edge of the Archipelago to the Labrador Sea is represented by only 12 stations, so it is relatively under-represented compared to the western half of the survey.

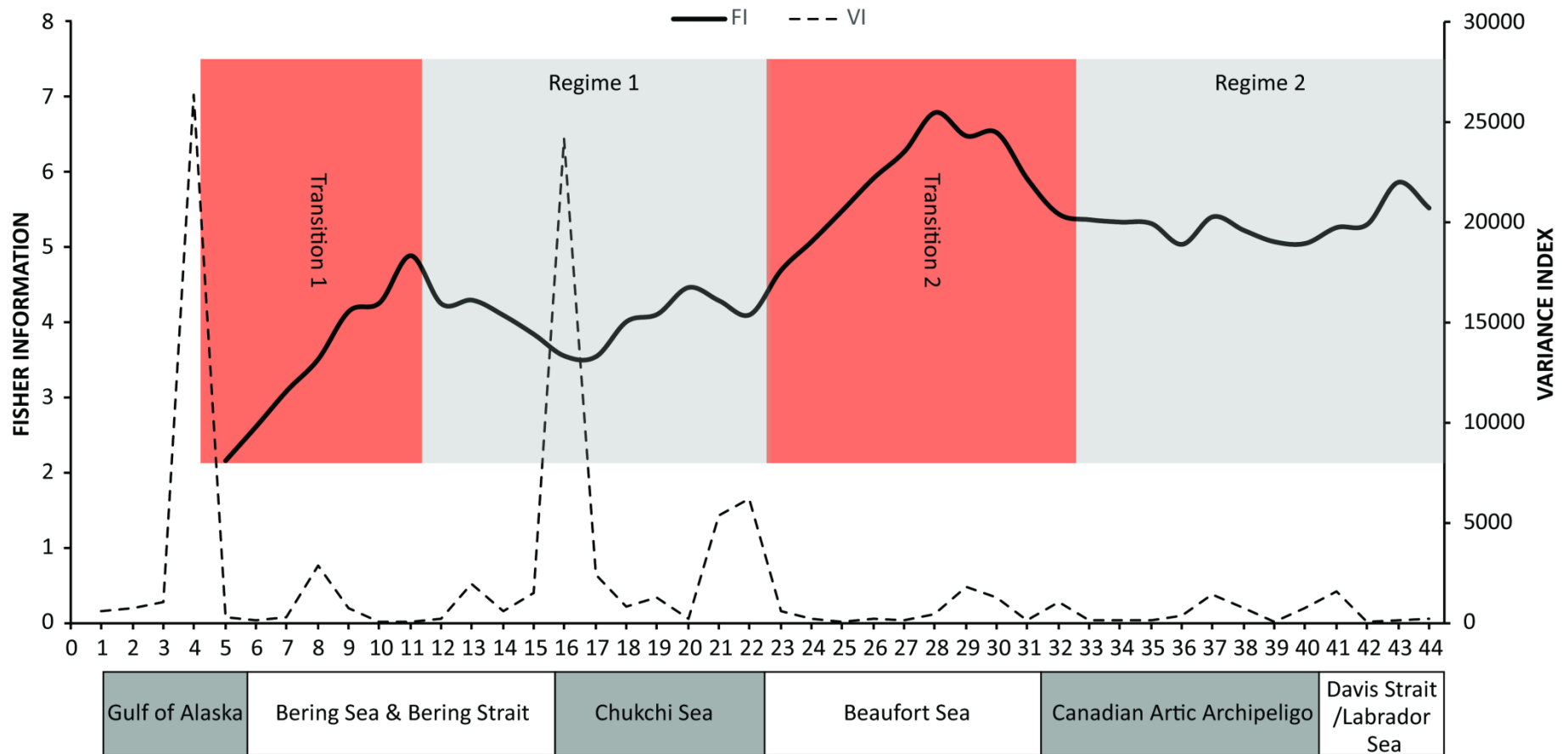


Figure 6.7 Fisher information (FI; bold solid line) and Variance Index (VI; faint dotted line) for zooplankton community data from transect of 44 sampling stations ordered from west to east along the x-axis. Because one FI value is produced per window, the first FI value is at route 5. Regimes and transition zones are shown as boxes drawn around the FI plotted line. The *a priori*-defined oceanic domains are under the x-axis, to see how well the location of the regimes identified by FI align with the oceanic domains identified in the literature.

Like the terrestrial case study, when the FI trends are compared to the traditional regime shift indicators, only the VI was able to provide sensible results (Figure 7). The Variance Index peaks at the boundary of the Bering Sea, the Chukchi Sea, and to a lesser extent the Beaufort Sea Shelf. However, it does not distinguish whether the increased variance denotes the beginning of a stable regime, or signals a transition zone. The descriptive statistics support an overall picture of change in community structure which reflects successive patterns of an ecoregion with high variability (i.e. high σ FI and cvFI) transitioning into a more stable regime (high μ FI, and low σ FI and cvFI) (Figure 8).

The multivariate analyses support the FI results, and suggest that the boundaries between the *a priori* defined ecological domains are soft, particularly between the Bering Sea and Chukchi Sea. When viewed in ordination space, the nMDS places the stations so they more or less flow from west to east along the arc, but there is also strong overlap in community structure at sampling locations near the edges of the domains (Figure 9; (stress value of 0.121 for 3 dimensions)). The cluster analysis (Figure 9; pruned to 6 clusters) divides the stations of the Bering Sea into two clusters, and places two of the Bering Sea stations in the Chukchi cluster, as well as fails to distinguish between the Canadian Arctic and the Davis Strait/Labrador Sea. The overall result is that the zooplankton communities do not have crisp boundaries which fully align with the *a priori* defined domains described in the methods, but have softer boundaries with considerable overlap in community structure between domains. Furthermore, FI communicates a richer story of community structure transitioning across space than either the nMDS or cluster analysis. However, unlike the BBS case study, the transition zones were marked by a rise in FI, as opposed to a

drop, which may suggest a possible slowing down of changes in community structure before the patterns destabilized and the system organized into a new regime. Further work on the underlying system dynamics would be instructive.

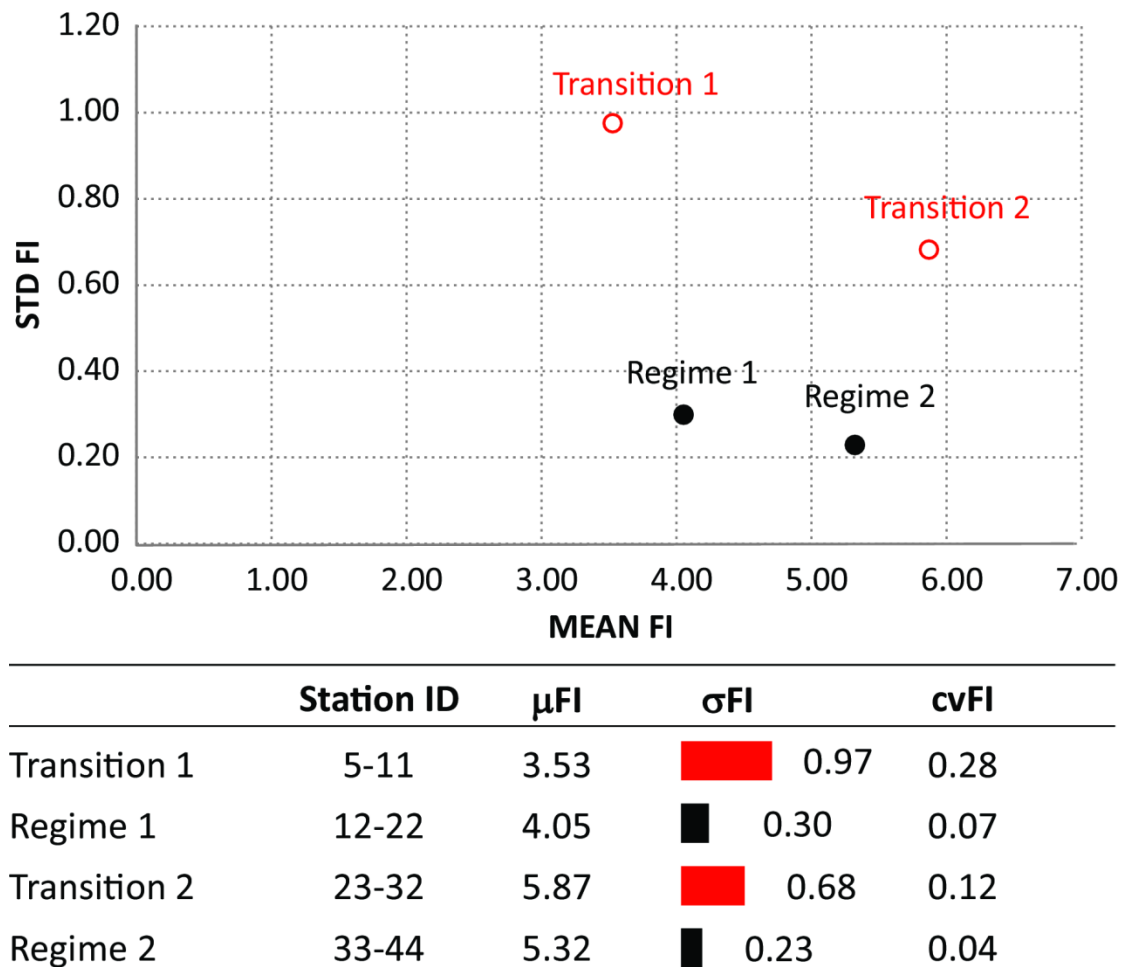


Figure 6.8 The stability of each marine regime over space, as defined by the mean (μFI), standard deviation (σFI) and coefficient of variation of FI (cvFI). While the two regimes are relatively stable with high μFI , low σFI and low cvFI , the transition periods exhibited the least stability. Note: Regimes reflect the domains identified by the trend in FI, **not** the regimes *a priori* identified using Carmack et al. (2010)) and Archambault et al. (2010).

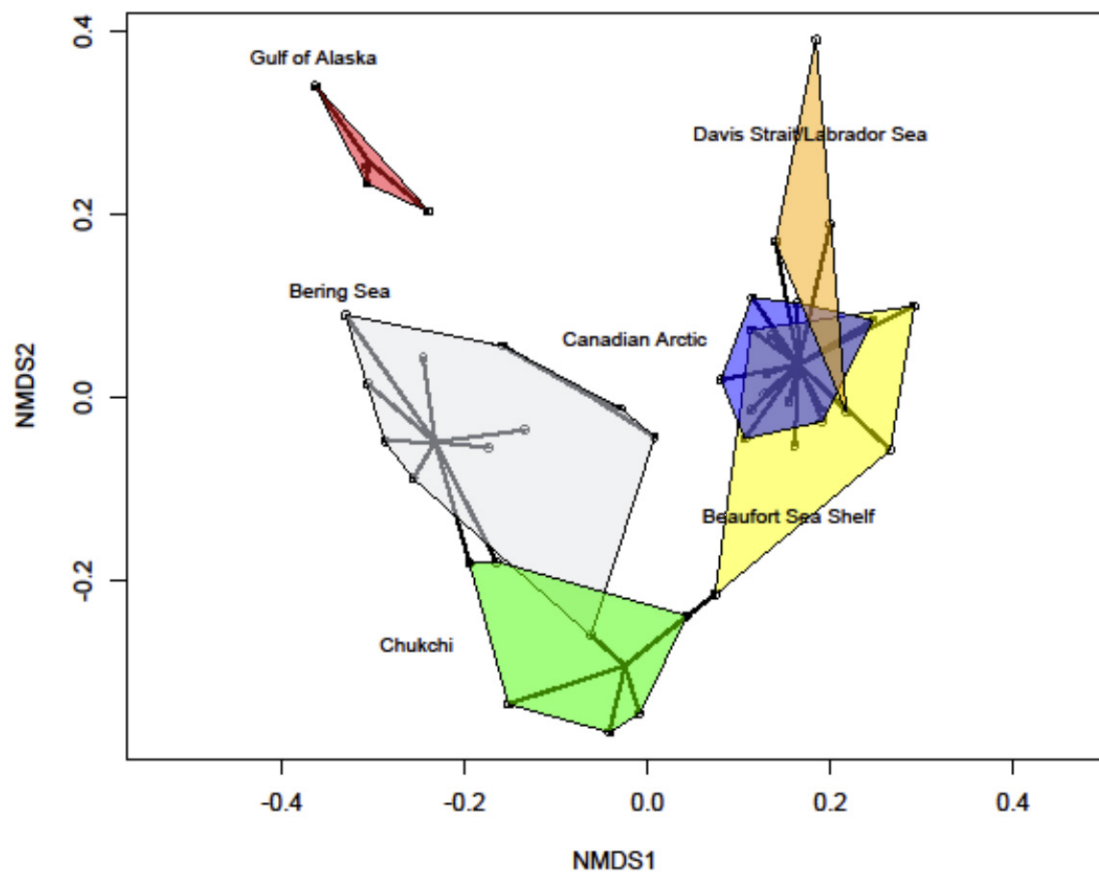


Figure 6.9 Ordination plot for the zooplankton community data ($k = 3$; stress = 0.121). The sampling stations are shown with open circles. The results of a cluster analysis (pruned to 6 clusters) are shown with black spiders, while the oceanic domains *a priori* identified from the literature are represented by the colored polygons. Both the nMDS and the cluster analysis fail to assign some sampling stations to the ‘correct’ oceanic domain for all domains except the Gulf of Alaska. ([Figure 6.9.pdf](#), 19KB)

Discussion

Detecting spatial regimes with Fisher information

Given animal community data, we found that Fisher information was able to detect spatial regimes and transitions between spatial regimes in both terrestrial and aquatic ecosystems, across regional scales (1900 and 12,000 kilometres respectively).

These studies were an important step towards determining the utility of FI in detecting spatial regimes in both aquatic and terrestrial systems, even given data limitations. In contrast, the traditional indicators we examined, such as variance, skewness, kurtosis, and critical slowing down, were unable to detect spatial regimes, though this was unsurprising as they are not suited for multivariate data. The VI helped to confirm general trends, but it does not reveal details about the regime dynamics that are useful for assessing the behavior of the system, e.g., whether there is a stable regime between two peaks, or whether changes in the VI are capturing a transition. Our results suggest that Fisher information can be a powerful, easy-to-use tool to assess regime shifts in animal (or other) community data, providing a biological link between anthropogenic disturbances such as land use and climate change and spatial shifts in ecological communities.

The ecological reality of community regimes

Our analyses demonstrated that the bird community boundaries only roughly coincided with the expectations of ecoregion maps. There are substantial differences between the potential vegetation underpinning the ecoregion classifications, and the actual spatial locations of stable avian communities. If FI were to fully coincide with the ecoregion maps, then we would expect to see a stable FI value through the center of each ecoregion, with evidence of increasing variability at the borders, indicated by declining FI. Instead, the High Plains had high variability in community structure throughout the core of the ecoregion. And rather than FI identifying three distinct Plains regimes, as per the ecoregion expectation, it identified two regimes, each of which straddled routes from the Central Plains. In other words, the avian community structure was simplified relative to ecological expectations, with a blurring of the

boundaries between what are considered distinct ecoregion types by US land agencies. Indeed, the difference in FI between regime 2 and regime 3 is such that the argument could be made that the entire Great Plains is one regime, with a slow but steady loss of order as one moves from west to east, corresponding with an increasing intensity of agriculture. The transitions to and from the Plains are both much steeper than that between the two Plains regimes, as would be expected.

The land cover summary (Table 1) supports the findings of FI as it demonstrates that the three prairie landscapes exist on a gradient of actual vegetative cover. As we move east from the High Plains to the Cornbelt Plains, the percent grassland cover drops dramatically from 60% to 5%, and the percent of row crop land cover rises from 14% to 74% (Table 1). The most significant changes occur between the High Plains and the Central Great Plains. These patterns are in contradiction to ecoregion maps (Omernik 1987; Bailey 2015), which hold the difference between the Central Great Plains and the Western Cornbelt Plains as much more fundamental (a Level I division) than that between the High Plains and the Central Great Plains (a Level III division). To the extent that the land use cover in each 400 m route buffer around the ~40 km route reflects on a gross level the land cover of each ecoregion, it seems likely that the heterogeneity within the Plains landscapes due to agriculture and grazing has been reduced.

Table 6.1 Land cover classification for a 400 m buffer around each 41 km BBS route. The dominant land cover type for each ecoregion is in bold. Note that Northern Lakes and Forest is roughly evenly split between Deciduous Forest and Woody Wetlands, evidence for the heterogeneity of the region.

Landcover Type	Southern Rockies	High Plains	Central Plains	Western Cornbelt	Northern Lakes and Forest
Open Water	0.01		0.01	0.01	0.04
Low Intensity Residential				0.02	
Deciduous Forest	0.14		0.02	0.03	0.25
Evergreen Forest	0.47				0.12
Mixed Forest	0.01				0.11
Shrubland	0.15				
Grassland/Herbaceous	0.18	0.61	0.20	0.05	
Pasture/Hay	0.02	0.04	0.08	0.12	0.10
Row Crops		0.14	0.66	0.74	0.03
Small Grains		0.13	0.02	0.01	
Fallow		0.07			
Woody Wetlands					0.28
Emergent Herb Wetland				0.01	0.04

*Only showing those categories for which at least one ecoregion has > 1%

The length of each transition zone is suggestive of soft, rather than the hard boundaries depicted on ecoregion maps (Bailey 1983; Omernik 1987). The long transition from the Cornbelt Plains to the Northern Lakes and Forest, which covered more than 400 kilometres, may be impacted by two factors: First, the final two routes in the Cornbelt Plains occur on the upward sweep of the transect and so are substantially more northern than the other Cornbelt Plains routes. Latitude is known to affect animal communities (Clergeau et al. 2006). Second, the first route in the Northern Lakes ecoregion technically falls into a narrow band of the North Central Hardwood Forest. This rapid shifting across three ecoregions is captured by FI as a long transition before the fourth regime begins. Finally, the higher cvFI and thus relative variability of FI in the fourth regime, which falls wholly within the Northern Lakes and Forest ecoregion, is possibly explained by the heterogeneity of the land cover, though it is also possible that further data points would reveal the fourth regime as another transition as the study ends at a geographic rather than ecological border. However, community structure in this ecoregion is likely more variable than in the other regimes because the landscape itself is more variable, as it is a patchy mosaic of water features and forest (Table 1).

The zooplankton data tell a similar story to the avian data. Although there is correspondence between zooplankton community structure, large scale oceanic structure, and regime transitions as detected by FI, some boundaries are less defined than *a priori* expectations. Domains thought to contain distinct communities, such as the Bering Sea or Beaufort Sea Shelf (Springer et al. 1989; Hopcroft et al. 2010; Pomerleau et al. 2014), appear to be transition zones between stable communities. The failure of both FI and the nMDS to distinguish between the Canadian Arctic

Archipelago and Davis Strait/Labrador Sea may be a function of inconsistent sample coverage. Further work examining how the frequency of sampling affects the power and sensitivity of FI is warranted.

The inability of FI to crisply distinguish between the Bering Sea and the Chukchi Sea is consistent with our understanding of the region as a mixing zone where Bering Shelf water mixes with water from the Anadyr current, which enters from the west, and Alaska coastal water, which enters the Bering Strait from the east (Coachman et al. 1975). These three water masses are believed to harbour unique zooplankton communities (Springer et al. 1989), and as the water masses do not mix until they pass through the Bering Strait into the Chukchi Sea, the zooplankton community contains a mixture of communities that differ from the southern Bering Sea and have high patchiness (Eisner et al. 2014; Pomerleau et al. 2014). As the transect enters the Beaufort Sea, there is a decline in both Pacific taxa and zooplankton community patchiness associated with the mixing of the three Pacific water masses and Arctic water, corresponding to greater similarity among samples and increasing dynamic order in FI. The expectation was that the Chukchi, understood to be a mixing zone of watermasses, would be identified by FI as a transition zone, while the Beaufort Sea Shelf would be a stable regime. Instead, the northern part of the Bering Sea and the Chukchi had a stable FI value denoting it as a regime, while the Beaufort Sea Shelf underwent a long and significant increase in dynamic order that never flattened sufficiently to qualify as a regime. This means that the variability in zooplankton community structure as the transect traverses the Beaufort Sea was much higher than that of the northern Bering/Chukchi Sea, despite the latter region consisting of a mixing zone of multiple water masses. The FI results

suggest that studies on dominant zooplankton species within each domain (Nelson et al. 2009; Walkusz et al. 2010; Pomerleau et al. 2014) may not strictly correlate to bigger picture studies which assess variability in community structure over space, or that zooplankton species compositional data or the way in which they are collected are not a good proxy for spatial regimes.

What Fisher information captures that multivariate analysis does not

The nMDS analysis largely aligned with the *a priori* ecoregion and oceanographic domain expectations, but was not always able to distinguish between ecoregions (the High Plains and Central Plains) or domains (Canadian Arctic and Davis Strait/Labrador Sea), though in the case of the zooplankton data, may be a function of insufficient sampling stations in those domains. Perhaps most importantly, the multivariate analyses are largely visual; ordination methods create their own space, and thus do not tell us about spatial shifts in the location of a community. Routes that were geographically farther away from each other tended to be more dissimilar than routes that were close together. However, this rather crude depiction of community structure does not tell us where the boundaries between communities occur, whether they are hard or soft, or if the soft boundaries are themselves ecotones with stable community structure. Furthermore, the approach does not provide any insight on the spatial extent of the transitions. The ability to assess whether or not a particular community is gaining or losing order over time could allow land use managers to anticipate a potential regime shift within a location, or document if community locations shift in space over time. That said, our ability to detect change using FI may be improved by employing post-hoc tests to assess trends in the index. Researchers have explored approaches such as cut-offs, Mann-Kendall

tests, and Bayesian methods to help reduce interpretive uncertainty (Heberling & Hopton 2010; Vance et al. 2015; González-Mejía et al. 2016), but these methods are still under development.

Idio- or non-idiosyncratic changes in animal community regimes?

To what extent can we expect changes in plant and animal communities to occur in a fashion detectable by monitoring and analytical methods like the one presented here? Our contention is that it will depend on whether or not species' response to anthropogenic change is idiosyncratic within and across taxa. If species' responses are fully idiosyncratic, then the patterns at the community level will become chaotic as a function of independent species' responses as anthropogenic impacts accumulate and intensify. Accordingly, tracking spatial regimes and the location of the transition zones between them would not be a useful activity for managers or scientists. There are, however, constraints on individual response such that pattern identification will remain useful and feasible on shorter timescales, though the possibility of no-analog communities seems highly likely for multi-decadal or longer time scales (Williams & Jackson 2007). In general, we expect to see changes in animal abundances in the short term as a response to climate change and anthropogenic influence, as opposed to changes in presence/absence. Changes may result from range shifts, as there is substantial evidence documenting vagile species recently shifting their ranges to track their climatic niche (Parmesan, 2006; Parmesan & Yohe, 2003; Tingley et al., 2009), but the rate of climate change is such that migration capabilities are unlikely to keep up with the rate of thermal change (Thuiller et al. 2008), and the ability to shift ranges is further impeded by habitat fragmentation, which has been shown to reduce range shift (Iverson et al. 2004;

Thuiller et al. 2008). As a result, range contraction due to a lack of suitable habitat and reduced survivorship within their original range is also expected (Davis & Shaw 2001; Parmesan 2006).

These issues confound the identification of ecological boundaries and our ability to track changes in boundaries over time. Fisher information can assist researchers and managers in tracking changes in the patterns of community structure associated with habitat types or biogeographical distribution areas, as well as the temporal dissolution of community structure as no-analog communities assemble over time. A substantial benefit to Fisher information is that it circumvents many of the difficulties currently present in defining ecological boundaries, such as problems of non-linear responses across ecotones, landscape fragmentation, and land use change in terrestrial systems, or the ephemeral nature of some oceanographic boundaries, as well as the vast spatial scales involved, all of which can be difficult to capture without exhaustive data collection (Strayer et al. 2003; Kent et al. 2006; Danz et al. 2012). Other researchers have discussed the challenges of tracking boundary region shifts as a way to monitor climate change, when, for example, little to no native vegetation remains (less than 5% of the original prairie in the United States due to land conversion), and critical structuring processes have been repressed or altered (natural fire regimes suppressed) (Danz et al. 2012). Fisher information allows for the simultaneous analysis of multiple, disparate variables and provides a synoptic approach that may allow for detection of ecological change and boundary shift without pre-supposing key taxa as bell-weather species of change. However, future studies wishing to estimate more precisely the location of boundaries and how they

may shift over time may also need to account for phenological/seasonal detection differences in the taxon under question.

We also propose that monitoring animal populations is more likely to reflect currently changing conditions and is easier than detecting variation in plant communities or oceanographic properties. Remotely-sensed data remain challenged to identify physically similar but floristically different species, and ground-truthing large ecological regions is unfeasible. Animal species' responses are likely to occur more rapidly than plants, as there can be a large mismatch between vegetation and climate change, with changes in vegetation lagging substantially behind changes in climate (Beckage et al. 2008). Long-lived species such as trees can exhibit ecosystem responses to land use and climate change at century-scales because of the spatial and temporal processes structuring forests (Starfield & Chapin 1996), while terrestrial animal species are more vagile and can act as a leading indicator of vegetation change, or of a change in climatic variables such as temperature. Furthermore, as we demonstrated, there can be significant differences between ecoregion mapping, which is based on potential vegetation as a function of geomorphology and soils, and the location of spatial regimes actually present after decades of land use changes. All of these issues make it critical to identify reliable spatially-explicit tools for mapping the effects of climate and land use change on biodiversity (Mokany & Ferrier 2011), and our research suggests that Fisher information can be one of those tools.

Conclusion

Our analyses confirmed that when using multivariate data, traditional early warning indicators are very difficult to interpret, and integrated indicators such as FI and VI more consistently detect regime shifts. We found that Fisher information

provided the clearest, most detailed, and interpretable signal of spatial regime shifts. Although the Variance Index did not provide clear signals as a stand-alone indicator, some congruent trends are found when the results are presented in conjunction with FI. Fisher information has the further benefit of being highly flexible in terms of the choice of variable selection and data input, and is able to detect a clear signal without the need for difficult-to-acquire high resolution data.

This research had the further benefit of highlighting the incongruence between terrestrial ecoregion maps, which are focused on ecological potential, and the ecological reality of community regimes given land use and climate change. The method presented would allow researchers to track both the shifting spatial locations of communities over time, as well as the change over time within a location, both of which are critical as the consequences of anthropogenic change manifests in community structure and dynamics over time and space.

We appreciate that for both systems analysed, a different taxa could show spatial regimes in different locations. Reptile or mammal community regime location may or may not overlap bird regime location, and the transitions between ecoregions may be more or less steep given the taxa under consideration. Neither mammals nor reptiles tend to be as vagile as birds, and their ability to disperse in response to climate or land use change is accordingly more limited. Further research evaluating the spatial regimes of other taxa and the extent to which they overlap bird and zooplankton species would be useful.

Finally, further studies that looked more deeply into community structure within a spatial regime could inform managers as to which subgroups of species are most dominant within each regime, while correlation analysis could identify the

subgroups of species responsible for driving the value of Fisher information within each regime, both of which would allow managers to objectively select subgroups of species to monitor as the primary indicators of ecological stability within a community.

CHAPTER 7 THE ADAPTIVE CYCLE: MORE THAN A METAPHOR

Introduction

The adaptive cycle and its extension to panarchy (nested adaptive cycles) was proposed as a metaphor and conceptual tool for understanding long-term dynamics of change in complex adaptive systems (CAS) like ecosystems and social-ecological systems (Gunderson & Holling 2002). As such, the concept has had uptake by researchers from a variety of fields (Bunce et al. 2009; Burkhard et al. 2011; Randle et al. 2014; Fath et al. 2015; Kharrazi et al. 2016; Thapa et al. 2016) despite the lack of empirical evidence demonstrating adaptive cycles in real data (though see Angeler et al. 2015b). However, work from a wide array of fields, focused on an even wider array of ideas—self-organized criticality, edge of chaos, regime shifts, sustainability, resilience, punctuated equilibrium, game theory and thermodynamics (Langton 1990; Lindgren & Nordahl 1994; Kauffman 1995; Bak & Boettcher 1997; Ulanowicz 1997; Aronson & Plotnick 2001; Jorgensen et al. 2007; Lockwood & Lockwood 2008; Scheffer 2009b) suggests that the adaptive cycle describes endogenously generated dynamics in complex adaptive systems that may reflect inevitable dynamics of CAS's as a result of the internal processes of self-organization and evolution over time. We review the multiple lines of evidence supporting the theory that adaptive cycles and panarchy may be common structure resulting from the fundamental dynamics of complex adaptive systems. We also detail the multiple paths by which researchers

could systematically and quantitatively look for signatures of panarchical dynamics in ecosystems, rather than relying on metaphor and largely qualitative descriptions.

Adaptive cycles and panarchy

An adaptive cycle describes system movement through a 3-dimensional state space defined by system potential, connectedness, and resilience (Figure 1), as originally developed by Holling and colleagues (Holling 1986; Gunderson & Holling 2002). System potential is concerned with the range of options available for future responses of the system; in ecosystems this can mean an accumulation of nutrients, resources, biomass, and diversity that provide a broad range of options for the future behavior of the system in response to change. Connectedness refers to the relationships between system elements and processes, and the degree to which elements are dominated by external variability, or by relationships that mediate the influence of external variability (Holling & Gunderson 2002). Finally, resilience refers to the degree of disturbance a system can buffer without moving into a new regime, or basin of attraction (Holling 1973). The stylized cycle consists of four phases defined by the four quadrants of the state space, but importantly, system movement through the phases is not rigid or predetermined. In the two front loop phases, *r* (exploitation) and *K* (conservation), there is a slow and gradual accumulation of resources and relationships. Systems tend to spend the most time here, and are often understood to be on a stable attractor, or at a quasi-equilibrium in which large-scale system features such as biomass are stable over time (Hatton et al. 2015; Allhoff & Drossel 2016). As the system moves from the *r* phase of exploitation into the conservation phase, potential and connectedness increase, but resilience shrinks because the high connectedness amongst system elements makes the system

vulnerable to cascading disturbances. In the two back loop phases, omega (release) and alpha (reorganization), dynamics are rapid as the system transitions to a new phase of exploitation. The omega phase is characterized by the rapid release of accumulated resources; for example, in ecosystems, the release of nutrients and biomass when a disturbance event such as fire, drought, insectivory or intense grazing triggers a collapse. This is quickly followed by a period of reorganization, such as when soil processes capture nutrients and pioneer species begin colonization processes (Holling & Gunderson 2002).

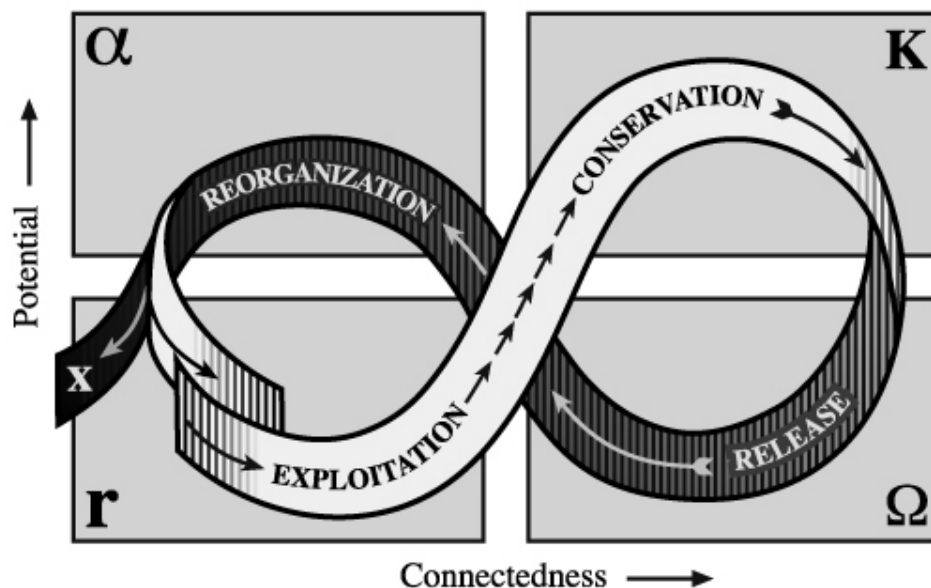


Figure 7.1 Phases of the adaptive cycle (from Gunderson & Holling, 2002)

Nested adaptive cycles with bi-directional cross-scale feedbacks are called a panarchy (Figure 2). A core hypothesis of panarchy is that the key processes that structure ecosystems occur at different ranges of spatial and temporal scales, often separated by orders of magnitude. Thus, the spatio-temporal scales of pine needle turnover on a pine tree are dramatically different than the geological scales of the

processes that drive where boreal forest occurs on earth. Research on the discontinuity hypothesis, closely related to the development of panarchy (Holling 1992; Nash et al. 2014a), demonstrated that ecosystems contain scale domains, or spatio-temporal domains over which key processes, ecological structure, and resources either do not change or change monotonically (Wiens 1989). Scale domains are separated by discontinuities, or scale breaks that represent a transition to a new set of structuring processes, as in the transition from photosynthesis structuring pine needles, to herbivory driving forest patch dynamics (Holling 1992; Nash et al. 2014a). Thus, adaptive cycles occur at each scale domain within the system, resulting in complex systems with multiple and nested domains of scales. At smaller and faster scale domains within a larger ecosystem, disturbances can drive cycling dynamics that are confined to those scales, while processes of renewal and regeneration depend on system memory at larger scales. Occasionally, disturbances can cascade up to larger and slower spatiotemporal scales, especially if those larger scale domains are in the K phase of their own adaptive cycle, as the accumulation of system potential in the form of standing biomass and bound nutrients shaped by high connectance between system elements renders it more vulnerable to cascading effects up the panarchy (Gunderson & Holling 2002).

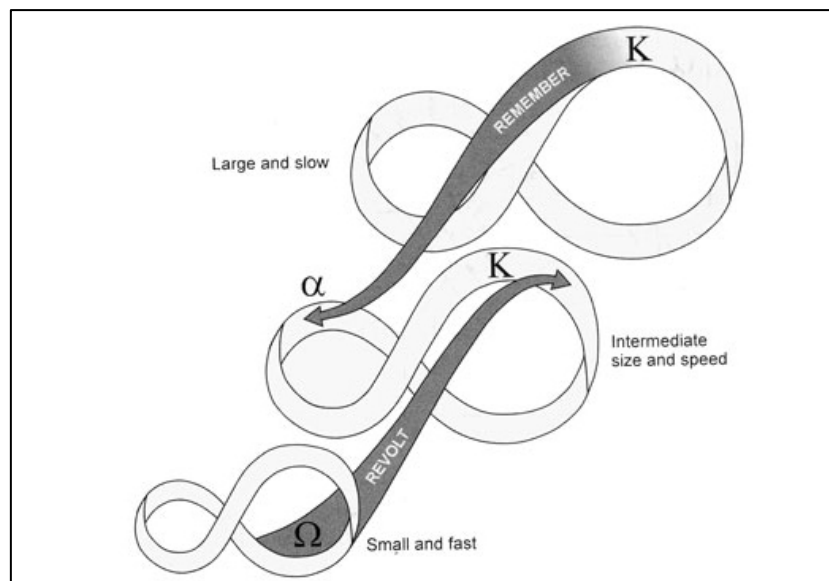


Figure 7.2 A panarchy. Three nested adaptive cycles with bi-directional cross-scale feedbacks (from Gunderson & Holling, 2002).

Clues from abroad: inference from other fields

These descriptions of cyclic system behavior intuitively apply to virtually any living, adaptable system, and the authors of the original panarchy volume (Gunderson & Holling 2002) both push back against the compulsion to see adaptive cycles everywhere, and utilize examples from a variety of economic, social, and ecological systems. Work on the adaptive cycle and panarchy has largely occurred within the confines of resilience science, a field of research connected to panarchy as both are part of a larger narrative of how to conceptualize, study, and manage complex ecological and social-ecological systems originally developed by Holling and colleagues (Resilience Alliance, 2017). However research in other fields also suggests that the fundamental dynamics of system development, maturation, collapse,

and reorganization captured by panarchy are endogenous dynamics in CAS's that reflect internal processes of self-organization and evolution over time.

Complex adaptive systems arise when systems are open; that is, they import energy and export entropy, and in the process of dissipating energy generate the essential characteristics of a complex system (Schneider & Kay 1994). Levin (1998) proposed that the essential elements of a CAS can be reduced to three things: “sustained diversity and individuality of components; localized interactions among the components; and an autonomous process where based on the results of local interactions, a subset of the components is selected for replication or enhancement (p. 432).” From these essential elements flow the other key features of a CAS: continual adaptation and introduction of novelty, non-equilibrium dynamics as a result of the dispersed and local nature of selection, the absence of top-down global control, and the emergence of hierarchical organization and other emergent phenomena (Levin 1998). Many have argued that when systems are driven by the same ‘physical principles and forces that drive self-organization in open, inorganic, far-from-equilibrium systems’, such as nonequilibrium thermodynamics (Kurakin 2010), then the patterns of emergence of structure and process should be generalizable across system types. If ecosystems and other complex adaptive systems are driven by the same fundamental rules of thermodynamics and physics then there are grounds for the premise that the basic phases of the adaptive cycle may be a feature of multiple types of complex adaptive systems.

Empirical evidence to support the contention that these dynamics are endogenous and primary to self-reinforcing, evolutionary systems comes from a range of fields. Non-equilibrium dynamics of change that are less extreme than fold-

bifurcations (regime shifts) can be difficult to model, either because data from real systems is highly labor-intensive to collect; non-linear dynamics are often intractable to mathematical resolution; or because reconciling mathematical predictions with experimental communities in a laboratory setting can be very difficult (Fussmann et al. 2000). Nonetheless, there is evidence to suggest that simple rules and local interactions between system elements can generate non-linear dynamics that fall into a range of behavior from fully ordered and at equilibrium, to chaotic and characterized by wildly oscillating fluctuations (Fussmann et al. 2000; Becks et al. 2005). In a study of predator-prey interactions in laboratory conditions, population dynamics included chaotic behavior, as well as stable limit cycles and coexistence at equilibrium (Becks et al. 2005). Foster and Wild (1999) used a non-linear logistic diffusion sigmoid curve to map the phases of self-organization in economic systems, which mirror the adaptive cycle, and Lindgren and Nordahl (1994) found that the shifting pattern of dynamics emerging from the tension between competition and cooperation in evolution in social systems creates a shifting pattern of dynamics where cooperative structures self-organize, grow, occasionally enjoy long stable periods, and then break up over time. The system is in a perpetual non-equilibrium state because of the trade off between competition and cooperation, and, importantly, complex and unpredictable patterns and structures emerged from an initial chaos. The patterns were cyclic and punctuated; over time a pattern emerged and stabilized until a mutation/innovation appeared that abruptly generated pattern collapse and reorganization. The cycling behavior of companies over time follows the adaptive cycle closely, as many companies jostle somewhat randomly for their niche, a small number grow explosively to a large size and dominate for sometimes decades, and

then inevitably crash and fail (Beinhocker 2006). While in ecosystems the players still standing after a crash then reorganize and begin the process over again in competition with opportunistic invaders, usually the same company does not re-enter the playing field after failing, but is replaced by a multitude of new, small start-ups, or previously subordinate companies that are competitively freed (Beinhocker 2006).

In archaeology, Marcus (1998) developed a dynamic model of social evolution that explains ‘cycles of consolidation, expansion, and dissolution’ (Parkinson & Galaty 2007) of geopolitical states which has since been shown to fit a wide range of archaeological communities, while work by Tainter (1988) demonstrates what can happen when the collapse phase occurs at the level of the panarchy, rather than at smaller-scale adaptive cycles (collapse of civilizations). Though Gunderson and Holling (2002) briefly discuss punctuated equilibrium as another example of adaptive cycles, Jain and Krishna (2002a, 2002b) modeled evolution in a simulated ecosystem and found cyclical dynamics as a result of endogenous interactions that correspond to both punctuated equilibrium and adaptive cycle dynamics. The parameter which drove the system through the phases of growth and collapse was the changing pattern of connectance between system elements, precisely as Holling predicted in his adaptive cycle.

Foundational work in complex systems theory also supports adaptive cycle dynamics as endogenous processes of complex adaptive systems. Work by early pioneers argued that there are a limited number of system states to which systems evolve. These states strongly parallel the 4 phases of the adaptive cycle, and despite criticism that these cellular automata and Boolean network modelling efforts were too mechanical to effectively capture the dynamics of real complex systems they

highlighted that given too much or too little order, systems can be trapped in states that lead to death because they are either too static or too chaotic to support the processes necessary to sustain self-organized, persistent structural hierarchies that can adapt and evolve to changing conditions (Figure 3)(Wolfram 1984; Langton 1986; Kauffman 1993; Ulanowicz 1997).

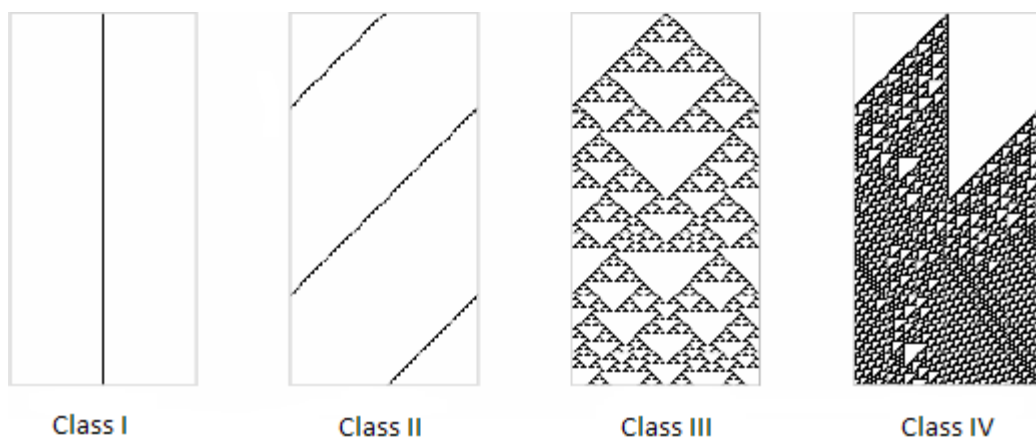


Figure 7.3 Wolfram's 4 classes of cellular automata end states. In Class I, evolution leads to a homogeneous state (limit points). In Class II, evolution leads to a set of separated simple stable or periodic structures (limit cycles). In Class III, evolution leads to a chaotic pattern (strange attractors). In Class IV, evolution leads to complex localized structures, sometimes long-lived (long transients) (adapted from Wolfram, 1984).

Langton (1986) proposed that systems therefore evolve to 'edge of chaos' behavior, where they are poised at the cusp of chaos and avoid falling into the traps of frozen order or full-fledged chaos. Furthermore, evidence suggests that systems at the edge of chaos are able to maximize information, entropy rate, and adaptation (Latora et al. 2000). Ulanowicz (1997) pushed back against the claim that the edge of chaos is a point or tiny region of state space, arguing that it is more appropriately viewed as a range or region of parameter space which he calls a 'window of vitality', and

subsequent work has borne this out (Zorach & Ulanowicz 2003; Nakajima & Haruna 2011; Benincà et al. 2015).

Edge of chaos dynamics are closely related to the theory of self-organized criticality, which argues that systems can self-organize to a point or region of state space that is a transition between order and chaos, where behavior exhibits power-law and/or fractal dynamics (Kauffman 1995; Bak & Boettcher 1997; Pascual & Guichard 2005). Schneider and Kay (1994) propose that life itself is a far-from-equilibrium dissipative structure, arising to poise at the cusp between low and high entropy (order and disorder) and this tension between opposing forces is mirrored in ecology, where the tension and trade-off between diversity and redundancy plays out in evolution, community assembly, and resilience (long-term persistence in a regime)(Page 2010). Studies from a broad range of fields have found edge of chaos dynamics and/or self-organized criticality (Bonabeau 1997; Turchin & Ellner 2000; Latora et al. 2000; Li 2000; Lansing 2003; Kurakin et al. 2007; Upadhyay 2009; Kitzbichler et al. 2009; Kong et al. 2009; Salem 2011; Nakajima & Haruna 2011; Chua et al. 2012; Benincà et al. 2015), but interestingly, not all systems stay there, as some systems show such dynamics for only a range of parameter space, or for a limited duration of time, or only larger system scales stay poised at criticality (Li 2000; Upadhyay 2009; Medvinsky et al. 2015; Lansing et al. 2017) while smaller scales experience collapse and renewal consistent with the other system states articulated by the early pioneers.

If, as has been argued, systems are tuned to evolve to criticality, where even small events can trigger a collapse or phase transition (Bak & Paczuski 1985; de Oliveira 2001) then it is far from obvious that all spatial and temporal scales of a complex adaptive system could be at criticality concurrently, as this would generate

severe instability as even small disturbances would constantly cascade up and down system scales. Instead, at ecosystem-level system scales and larger, we tend to see stable quasi-equilibrium behavior which can persist long enough that it led earlier ecologists to assume that deterministic successional behavior and equilibrium dynamics was the norm (Clements 1936). Brunk (2002) argues that systems require time to rebuild the structure that allows the transmission of disturbance. In forests, for example, it takes time to regrow the biomass that becomes the fuel load which can spread fire throughout the forest, rendering it unlikely that a system can stay poised at SOC at the system level unless regular collapses at smaller spatial and temporal scales occur with sufficient frequency to prevent disturbances from cascading up to the largest scales of the system. Similarly, Plotnick and Sepkoski (2001) argue that extinction and origination processes, which Bak and Sneppen (1993) claim fit power-law behavior and SOC, are better explained by hierarchical and multiplicative processes operating over multiple distinct ranges of scale. This means that at only at certain scales and certain periods in extinction/origination processes would there be behavior typical of SOC.

Another body of evidence suggesting that adaptive cycles may be generic and ubiquitous features of complex systems comes from researchers who have tried to bridge the gap between fundamental theory in non-equilibrium physics and chemistry, and the dynamics of ecosystems or other complex adaptive systems over space and time (Schneider & Kay 1994; Ulanowicz 1997; Jørgensen & Fath 2004; Beinhocker 2006; Kurakin 2011). One basic tenant that has emerged is that systems accrue complexity over time as processes of self-organization generate discontinuous, hierarchical layers of structure that dissipate more energy (Schneider & Kay 1994;

Jørgensen & Fath 2004). Furthermore, system development moves towards ‘increased order, organization, and storage of usable energy in sequential phases that see first biomass, then networks, and finally information (in terms of genetic complexity) increase’ (Fath et al. 2004; Jørgensen et al. 2016). Complexity and order evolve from relative simplicity and disorder under the influence of “periodic but transient setbacks in the form of organization relaxations and restructuring” (Kurakin 2011). These authors describe detailed dynamics of change in complex adaptive systems via various applications of thermodynamics (exergy, infrared thermal measurements and electron and proton transport in autocatalytic processes)(Schneider & Kay 1994; Jørgensen & Fath 2004; Kurakin 2011) that fully align with panarchy, although they place less emphasis on the stages of collapse and renewal. They argue that setbacks to this trajectory of increasing complexity have occurred at all spatial and temporal scales (e.g. from a small forest fire to mass extinctions to the fall of prior civilizations), but have not changed the fundamental trajectory of increasing complexity over time; the players may come and go, but the organization of relationships tends to be preserved and evolve (Kurakin 2011). Setbacks in this trajectory towards increased complexity are therefore temporary and of little import. However, we argue that externalizing setbacks as temporary impediments to be overcome rather than necessary for long term persistence and renewal through innovation and adaptation is problematic. Furthermore, the relative impact of ‘setbacks’ depends on the timescale under consideration. For example, social and economic systems at the global scale are increasingly complex (more structure and information content as in Ulanowicz 1997), but many ecological systems are at risk of simplification as anthropogenic degradations accumulate, rapid species extinctions

reduces the diversity necessary for systems to retain and build complexity, and climate change drives an increased risk for system-level regime shifts. Alternate regimes can be simpler, more homogenous systems as a result of missing crucial elements that allow it to reorganize into a similar state after a disturbance. When viewed at geological timescales, it seems likely that processes of thermodynamics, self-organization, and evolution will resume the inexorable march to increasing complexity. That is small comfort, however, for humans in the 21st century, given the timescales under consideration.

Collectively, these different theories on endogenously driven cycling dynamics of change are the backbone of our argument that nested adaptive cycles are generic and ubiquitous dynamics of complex adaptive systems. They inform our series of propositions and testable hypotheses .

Our propositions

#1 If nested adaptive cycles are innate dynamics of complex adaptive systems, there ought to be generic, measurable signals of such dynamics

Our most general proposal is simply that a panarchy, or nested adaptive cycles, reflect the inevitable dynamics of CAS's as a result of the internal processes of self-organization and evolution over time. Even in the absence of anthropogenic forcing or exogenous drivers, CAS's can move among the phases of the adaptive cycle as a result of internal dynamics that are driven by self-organization and evolution, and that research on self-organized criticality, punctuated equilibrium, game theory, artificial intelligence, and thermodynamics support this hypothesis (Kauffman 1993, 1995; Lindgren & Nordahl 1994; Aronson & Plotnick 2001; Jørgensen & Fath 2004; Lockwood & Lockwood 2008). The movement of a system

through the phases of the adaptive cycle could also be triggered by exogenous factors, but regardless of the trigger the trajectory of movement will be sensitive to initial conditions as well as the relative resilience of the system as it shifts from one phase to another. Because complex adaptive systems by definition evolve, the qualitatively similar system dynamics described in a variety of systems are likely the result of evolution in a thermodynamically open complex system. We propose, therefore, that there ought to be system signals that can be used to track a system's developmental trajectory that are consistent across varied system types.

#2 Tracking system change at scale domains will improve our ability to identify and predict dynamics of system change over time

Panarchy allows researchers to explicitly examine the scales at which dynamics of growth, maturation, collapse and renewal occur, so provides a framework for evaluating whether cross-scale feedbacks buffer or amplify collapse across the nested adaptive cycles of the system. Amplification can lead to a system-level regime shift during the renewal phase which manifests as movement to another attractor as the system reorganizes (Scheffer 2009b). Regime shifts in ecological and social-ecological systems are an active research field. Typically, regime shifts at the system level, such as a shallow lake, grassland, or coral reef system, are examined for movement between alternative stable states. However, cycling dynamics at smaller spatial and temporal scales within the system can either buffer or amplify disturbances, so connecting the probability of a system-level regime shift to the dynamics of adaptive cycles within system scale domains would be of value. For example, studies suggested that the Baltic Sea had undergone a regime shift (Österblom et al. 2007; Möllmann et al. 2009), but Yletyinen et al. (2016) argued that

the shift was not system-wide and involved only a limited number of species; the difference between a regime shift at one scale domain versus the system is not trivial. A primary distinction between panarchy and other models of system change is that panarchy explicitly incorporates differences between the spatial and temporal scales of key processes. We argue that finding system signals which track dynamics of change at explicit and objective scales would improve our ability to identify and predict potential cascading effects of disturbances. Systems should evolve to edge of chaos/SOC dynamics and cycle through periodic stages of release and reorganization without the interference of any human generated disturbances, but it is clear that human-forced perturbations could drive a system or adaptive cycle(s) nested within a system through cycles of creative destruction and reorganization far more frequently than power law behavior might predict. Understanding and quantifying the risk of cascading disturbances is critical, but not feasible unless we can identify simple metrics that capture the state of development of a system with data that is realistic to acquire.

#3 Self-organized criticality and/or edge of chaos dynamics are characteristic of one phase of the adaptive cycle

We hypothesize that the conservation (K) phase of an adaptive cycle may well operate at SOC or the edge of chaos, but only if cycles of collapse and renewal occur with sufficient frequency at smaller spatial and temporal scales (Brunk 2002; Gunderson & Holling 2002). For example, if the hierarchy of nested adaptive cycles in a system were identified using discontinuity theory as per Nash et al. (2014a), then we would expect to see that as systems develop and mature within and across scales, power law behavior and edge of chaos dynamics will increase from ‘weak’ to

‘strong’, peaking in the K phase of development, consistent with theory (Brunk 2002), and that edge of chaos/SOC is more likely to be persistent at larger spatial and temporal scales.

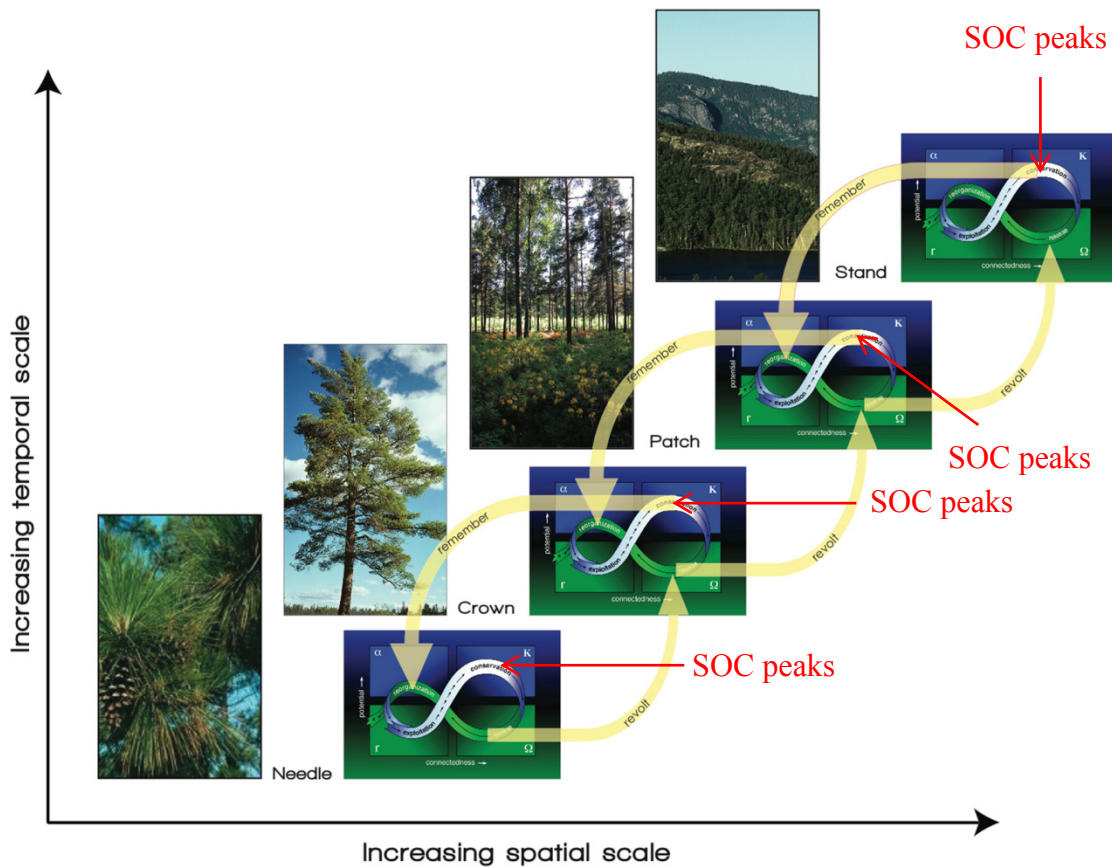


Figure 7.4 A conceptual diagram of nested adaptive cycles for a pine-dominated ecosystem. Self-organized criticality should peak at the height of the conservation phase of the adaptive cycle. Since the spatial and temporal scales increase at each level of the hierarchy, the forest system at the highest level in the panarchy should spend the most time at SOC. Adapted from Allen et al., 2014.

Ecology currently has early warning indicators of an impending regime shift, though their ability to explain historical behavior is better than their ability to predict the probability of a future regime shift (Seekell et al. 2011; Lindegren et al. 2012; Perretti & Munch 2012; Batt et al. 2013). Similarly, it makes sense to try to reduce a system to variables that can represent the state of the system as a whole because we often lack time series data on complete food web topologies or ecological networks.

Potential signals of adaptive cycle dynamics

We discuss a series of possible parameters that could represent a system signal of dynamics of behavior and change. Many of these have been developed and/or explored by other researchers for precisely that purpose (Burkhard et al. 2011), but with the goal of representing system behavior at the largest spatial and temporal scale, whereas we argue for the value of understanding dynamics of change within and across the scales of the system. These signals are thermodynamic metrics, and include exergy, ascendancy, infrared, and Fisher Information; network theory and connectance; and biomass.

Thermodynamic metrics

A variety of indicators use principles of thermodynamics to capture system development and change, but perhaps the most well-known are exergy (Mejer and Jorgensen), ascendancy and its related indicators (Ulanowicz 1997), infrared (Schneider & Kay 1994), and Fisher Information (Fath & Cabelas 2004; Karunanithi et al. 2008). Exergy measures the difference in entropy between equilibrium and an actual state. Since ecosystems operate far from equilibrium, measuring ecosystem exergy reflects the total amount of energy stored in organic structures (Ludovisi 2009). Exergy equations take into account information/structure, and concentration, and indirectly account for the manner in which biological matter is distributed among ecosystem compartments, typically by using carbon as the energy currency and genetic complexity as the information (Ulanowicz 1997; Scharler 2012), such that more biomass of more complex organisms will cause exergy to rise (Fath & Cabelas 2004). The detailed data required to calculate exergy for an equilibrium system (used

for comparison and necessary for the calculation) as well as the system of interest is formidable. Exergy by itself is disconnected from a larger understanding of resilience, as the extinction of lower-order species with less genetic complexity and an increase in abundance of higher-order organisms with more complexity can drive an increase in exergy (Fath & Cabezas 2004), but will also reduce functional redundancy and future adaptive capacity. From the perspective of the adaptive cycle, an increase in exergy in this scenario would equate to reduced resilience and reduced potential, and thus when exergy is calculated at the system level, it does not sufficiently capture critical system features. Furthermore, developers of exergy-based indicators tend to use reductionist terms such as stable ‘climax’ community succession dynamics and downplay or ignore collapse and renewal dynamics (Ludovisi 2014). However, were exergy to be calculated for each scale domain and thus for the complete nested set of adaptive cycles, it could potentially capture sufficient information about system dynamics to provide a picture of system change and development through time.

Ascendency theory (Ulanowicz 1997) quantifies change in system dynamics by using information theory to measure growth and structure in food webs, where growth is an increase in system activity or total system throughput, and structure is the mutual information contained in the trophic flow. Ascendency, when coupled with overhead, which captures system redundancies and the material for adaptive capacity, is a process of growth and maturation in ecosystems that fully parallels panarchy. In fact, Ulanowicz used ascendency theory to test the adaptive cycle and concluded that they are fundamentally telling the same story (1997). However, panarchy explicitly addresses the notion of cycling dynamics occurring at multiple

domains of scale, and via the discontinuity hypothesis provides a method for detecting scale domains (Holling 1992), whereas ascendancy theory only touches on feedbacks across levels in the hierarchy and does not explicitly model or account for them. Furthermore, it fails to substantively treat collapse and renewal as integral and necessary processes that are both unavoidable and critical for system resilience and persistence; the stages of maturation only briefly acknowledge that there are ‘temporary setbacks’, and downplay the possibility of collapse occurring at large scales when a system has reached senescence (Holling’s K phase). In an application to national economies, the authors write, “The senescent stage is in some systems usually followed by reorganization or by recycling after which a new qualitative state of immaturity and growth emerges. There are, however, two possibilities for complex systems to escape recycling, at least temporarily” (Matutinovic et al. 2016). That is a serious caveat to throw out and immediately move past, as they do not discuss time scales or the fact that collapse in some form is inevitable. The failure to treat collapse and renewal as integral, endogenously driven and necessary processes that are critical for system resilience and persistence at larger spatiotemporal scales is a limitation of the theory. Furthermore, any theory that views disturbances as external to a system will be constrained in its ability to explain and predict future behavior. Such assumptions are particularly dangerous because they can permeate research choices that in turn can lead to misleading results; for example, Matutinovic et al. (2016) trim their economic data to capture only ‘trends that are not disturbed by exceptional geopolitical events or the last major recession’. This is reminiscent of reductionist assumptions of equilibrium dynamics and deterministic successional trajectories towards climax communities that get momentarily ‘disturbed’ by external events.

And finally, although Ulanowicz's (1997) rigorous and quantitative ascendancy theory captures system development, the data demands of fully realized food webs are intense and only provide a snapshot of ecosystems at one point in time. While tracking system development or dynamics of change via ascendancy and overhead will provide highly valuable insight into the trajectory of dynamics, the feasibility of doing so is low. A simpler signal that nonetheless represents dynamics either within a scale domain (at the scale of one adaptive cycle) or at the system level (the highest-order adaptive cycle within the system of interest) would therefore be of high value.

Infrared is a thermodynamic metric proposed by Schneider and Kay (1994) as a test of their proposition that complex systems such as ecosystems should increase their total dissipation over time and become more complex, whereas simple or degraded systems should dissipate less energy. They argue that "more mature systems should degrade incoming solar radiation into lower quality exergy", resulting in lower reradiated temperatures (lower airborne infrared thermal measurements). However, as Fath et al. (2004) point out, "ecosystems are complex adaptive systems, and as such one would expect the thermodynamic properties of the ecosystem to change during development". It is now understood that while more mature systems dissipate more exergy than less mature or degraded systems, exergy dissipation eventually plateaus while system maturation continues and is reflected in other thermodynamic metrics such as total energy throughflow and system exergy storage (Aoki 1995; Fath et al. 2004; Ludovisi 2014). As with exergy and ascendancy, understanding infrared in terms of the expectations of nested adaptive cycles would address current shortcomings; in other words, while Schneider and Kay's hypothesis that maturing ecosystems will continually increase total dissipation as expressed by

infrared may only be correct for the renewal and exploitation phases of the adaptive cycle, tracking changes in infrared within scale domains could nonetheless be an effective signal of ecosystem change over time. However, doing so for real ecosystems will require evaluating infrared within scale domains of ecosystems, something that is conceptually only feasible for vegetation systems, and would require developing techniques to identify scale breaks in vegetation systems.

Finally, Fisher Information is a measure of the amount of disorder contained in any given parameter or system characteristic, and is based on the probability of observing a system state (Fath & Cabezas 2004; Sundstrom et al. 2017). It has been used recently to detect spatial and temporal regime shifts in ecosystems (Spanbauer et al. 2014; Eason et al. 2014; Sundstrom et al. 2017) but has the potential to track system change as ecosystems move among the phases of the adaptive cycle because the degree of order can be reflected in patterns of species richness, abundance, functional richness, growth rate, connectance, and complexity (genetic), all of which are anticipated to change in systematic ways among the phases of the adaptive cycle. Whereas a drop in Fisher Information indicates a loss of order or pattern in the data from unstable dynamics and a loss of resilience, as we would expect during the collapse phase of the adaptive cycle, a rise in order indicates less change and possible movement to more consistent patterns, as we would expect in the growth phases, and a stable value for Fisher Information would occur during the conservation phase where the system spends the most time in a stable regime (Fath & Cabezas 2004). Because Fisher Information can handle any kind and amount of multivariate data, there is the opportunity to exploit a variety of data types that characterize system

dynamics in order to explore changes in Fisher Information over time and within scale domains.

Network theory/ Connectance

Network theory is commonly used to examine ecosystems as ecological networks, where each species is typically a node in the network, and the relationships between nodes is captured either via topographical features such as connectance (the number of other species to which a species is connected), or flows of energy or matter (Woodward et al. 2005; Ludovisi & Scharler 2017). Scale is often only an indirect feature of network analyses, either when species are classified by trophic levels, which can be a crude classification of scale (such as O’Gorman *et al.* 2012), or when organism body size is embedded in the network (Woodward et al. 2005). Although Holling (2002) did not reference network studies in his explication of adaptive cycles and panarchy, connectedness is an axis in the graphical depiction of an adaptive cycle. His depiction of connectedness is more akin to topological studies than flow network studies such as ascendancy theory (Ulanowicz 1997), as it focuses on connectivity between system elements, and how it is related to the degree to which system elements are influenced by external variables. Low connectivity between elements means their behavior is primarily controlled by external variability in processes, whereas high connectivity between system elements can act to strongly mediate and buffer external variability. However, high connectivity between system elements also renders the system more brittle and vulnerable to collapse (Ulanowicz 1997), because the degree to which nutrients are bound up in existing pathways and relationships between elements reduces the system’s ability to “sample alternative and potentially

better configurations” (Kurakin 2007). Tracking connectedness at each scale domain and across time may therefore be a robust signal of changing dynamics.

More recent studies suggest that highly complex food webs (networks) can be simplified to just a handful of functional groups that describe the types of direct and indirect interactions species have, and that these functional groups are well predicted by body mass (Kefi *et al.* 2015; Kéfi *et al.* 2016). It may be possible, therefore, to understand changes in network metrics like connectance or the number of trophic and non-trophic interaction types within scale domains in order to track system change over time. Since many interactions would naturally cross scale domains (in general, predators are larger than prey), it is not immediately clear how to calculate these metrics when partitioned by scale domains. Furthermore, as with calculating flows in metrics such as ascendancy, the data needs are fairly prohibitive because of the extent of monitoring and expert knowledge needed to populate these food webs (for example, see Kefi *et al.* 2015; Kéfi *et al.* 2016). Such efforts are likely to have a high reward, however, as the need to integrate network theory, which is focused on relationships between network elements and therefore accounts for scale only indirectly, and resilience theory via the discontinuity hypothesis, which is focused on the scales at which species and processes operate, is a ripe topic for research. Jorgensen *et al.* (2016) has argued for the need to integrate vertical and horizontal topology in network studies by bringing together hierarchy theory with thermodynamic theory via networks, but his understanding of hierarchy theory rests solely on levels of organization, rather than the more objectively defined scale domains driven by pattern and process that underpin discontinuity theory (Holling 1992)

Biomass

Perhaps the simplest possible signal of dynamics of change is biomass. During the reorganization and exploitation phases, biomass is expected to accumulate, and then plateau during the conservation phase when connectivity and recycling of nutrients and material increases. In a resilient system, system-level biomass should remain relatively stable while collapse and reorganization phases play out at smaller spatial and temporal scales, resulting in increased variability in biomass at the particular spatial and temporal scales of the disturbance as compensation processes occur. Changes in biomass in both flora and fauna ought to reflect movement among the phases of the adaptive cycle within scale domains, and could be converted to a measure of carbon similar to exergy analyses in order to have common currency to modeling of stocks of carbon in vegetation and animal species among scale domains and across time (Scharler 2012). Furthermore, other features of resilience such as functional diversity and functional redundancy, which mirror Ulanowicz's 'overhead' and provide the buffering capacity that prevents system-level regime shifts, can be readily incorporated into models of changing biomass at scale domains, merely by partitioning biomass within scale domains by functional groups (Peterson et al. 1998; Forys & Allen 2002). Understanding how biomass changes across scale domains, such as rate of increase in biomass, captures the basic thermodynamic changes that drive system growth, development, collapse and renewal (Kurakin 2010). Measuring this, however, will require two challenges to be met first.

The first challenge lies in our ability to detect scale domains in ecological systems. Typically, researchers identify discontinuities in animal body mass distributions for a specific taxa. Discontinuity theory argues that ecological

processes, and therefore ecological structure, occur at discrete and limited ranges of scale (Holling 1992). Since animals forage and interact with their environment in ways that are highly allometric with body mass, animal body masses fall into size classes, separated by discontinuities, that reflect those spatial and temporal scale domains of process and structure (Holling 1992; Nash et al. 2013b; Raffaelli et al. 2015). In short, animal body mass distributions are lumpy, consisting of groups of similarly-sized organisms that are separated by gaps, or scale breaks, where there are no species. Discontinuity researchers have used a variety of methods to identify scale breaks in animal data (Allen 2006; Nash et al. 2014a; Raffaelli et al. 2015), but the vast majority of discontinuity analyses use rank-ordered body size data of a single taxon, such as birds or mammals, and furthermore, only rarely have researchers identified scale breaks in ecological structure (Nash et al. 2013b). To our knowledge, only Holling (1992) in his original presentation of the discontinuity hypothesis compared the location of scale breaks found in multiple taxa concurrently. Yet any effort to understand ecological change at adaptive cycles across multiple scale domains requires the identification of scale breaks and scale domains in multiple taxon concurrently, something that is feasible but has not yet to date occurred.

Second, finding discontinuities in ecological structure (such as vegetation, coral reefs) remains a major challenge. Virtually all the research on the various thermodynamic metrics, with the exception of Fisher Information, has been conducted on aquatic systems and only rarely on terrestrial (Lu et al. 2015), presumably because they are easier to sample and have faster time scales. The fundamental difference between what we propose and other efforts to track system dynamics of change is that we argue for the need to track system dynamics at scale domains, and can leverage

existing theory and methodology when looking for scale domains in animal communities (Holling 1992; Allen & Holling 2008). However, our ability to find objective size classes in ecological structure remains limited to a few attempts to find breaks in the fractal dimension (Morse et al. 1985; Li 2000; Nash et al. 2014b), while most researchers fall back on pre-defined spatial scales, as in Lu et al. (2015) who survey vegetation plots at 1 m² for herbs, 25 m² for shrubs, and 100 m² for trees in a forest exergy analysis. The recent application of light detection and ranging (LiDAR) technology in ecology (Lim et al. 2003) has the potential to transform our ability to find scale breaks in vegetation, as the airborne scanning laser provides 3D scanning of vegetation, improving our ability to estimate standing biomass and capture multiple components of vegetation structure (Lefsky et al. 1999; Asner & Mascaro 2014; Coops et al. 2016), including the potential to calculate the fractal dimensions of forest vegetation (Yang et al. 2015). However, given the timescales of the longest-lived tree species, temporal data that captures the largest and slowest spatial scales in forest systems, in particular, will not be possible, making it difficult to understand dynamics of change at the scale of forest ecosystems.

Finally, changes in total amount of biomass at scales may be less significant than changes in the rate of growth. Flow rates in other complex adaptive systems have been shown to more accurately predict the state of a biological system than do concentrations (Kurakin 2009). Work on eco-exergy flows in forest plantations suggest that growth rates systematically vary over the course of development (Lu et al. 2015), though the short temporal span of the data (20 years) only covers the reorganization and exploitation phases of the adaptive cycle. Long-term data from terrestrial vegetative systems would be necessary to test these hypotheses.

Conclusion

Although the adaptive cycle and panarchy theory are conceptual and qualitative, important aspects of the theory have been empirically validated. A main premise of Holling's argument (2002) was that nested adaptive cycles occur at non-user defined scale domains but at specific ranges of spatial and temporal scales structured by a few key processes, and evidence has accumulated to support this (Allen & Holling 2008; Wardwell et al. 2008; Sundstrom 2009; Nash et al. 2014a; Spanbauer et al. 2016). Researchers within and without ecology have found panarchy a useful way to frame questions regarding dynamics within their systems. Concepts like self-organized criticality, edge of chaos, power-law behavior, ascendancy theory, thermodynamics, information theory and more all tell a narrative of system dynamics and behavior that are of a piece with panarchy theory.

We are proposing that the adaptive cycle reflects the inevitable dynamics of complex adaptive systems as a result of the internal processes of self-organization and evolution over time. We argue that because complex adaptive systems by definition evolve, the qualitatively similar system dynamics described in a variety of systems are the result of evolution in a thermodynamically open system, and as such, ought to manifest in signals of system development and change that can be tracked across the spatial and temporal dimensions of a system in accordance with the theory of nested adaptive cycles.

Our interest, therefore, is in system-level properties that remain stable *because of*, not *in spite of*, dynamics of change at smaller and faster spatial and temporal scales. None of the metrics or indicators proposed here (exergy, ascendancy, Fisher Information, network metrics, biomass or rate of growth) are based on a fixed species

identity or a particular community structure beyond how species identity is related to rates of energy consumption, functional role, or type of interactions with other species. As Kurakin (2009) explains, “what is preserved are the spatio-temporal relationships between individual components, i.e. a certain organizational structure-a form-but not individual components. Members come and go, but the organization persists”. Understanding system development and change over time will help us more effectively maintain such organization over timescales relevant to human lifespans.

CONCLUSION

This dissertation spanned a variety of data types from ecological to economic systems and concentrated on core ideas central to the notion of ecological resilience in complex adaptive systems. These core ideas revolve around scale and emergence, and are captured in Holling's discontinuity hypothesis, the closely related concept of panarchy, and resilience as an emergent phenomena. The analytical and conceptual chapters sought to extend these core ideas conceptually, and then test some of those extensions analytically.

In Chapter 1, I proposed that the discontinuity hypothesis and its extension in the cross-scale resilience model is relevant to other complex adaptive systems, and described how they can be used to identify and track changes in system parameters related to resilience. I explained the theory behind the cross-scale resilience model, reviewed the cases where it has been applied to non-ecological systems, and discussed some examples of social-ecological, archaeological/anthropological, and economic systems where a cross-scale resilience analysis could add a quantitative dimension to our current understanding of system dynamics and resilience. I argued that the scaling and diversity parameters suitable for a resilience analysis of ecological systems are also appropriate for a broad suite of systems where non-normative quantitative assessments of resilience are desired. Too many fields, including ecology, study critically important system features such as system persistence, function, and collapse without taking into account scales. Even within ecology, there

are extensive fields such as network theory or biological/functional diversity-ecosystem function studies that ignore or fail to take into account the role of scaled processes and their relationship to properties that emerge at the system level. Writing this chapter highlighted the need for methods to explicitly account for scales. Despite the challenges and limitations of the discontinuity hypothesis and cross-scale resilience model, they nonetheless provide an avenue for tackling scaling issues when trying to account for, predict, or explain system behavior and dynamics.

In Chapter 2, I applied my argument from Chapter 1 to cross-national economies as a complex adaptive system and tested whether global economies have discontinuous size distributions, a signature of multi-scale processes in complex adaptive systems. I contrasted the theoretical assumptions underpinning this methodology with that of the economic convergence club literature, and detailed the ways in which the traditional convergence club literature fails to substantively address the non-equilibrium realities of economic systems. I found that the size distributions of economies are discontinuous and that there are persistent patterns of aggregations and gaps over time, particularly in the tails of the data, suggesting that there are scale domains of structuring processes that act as basins of attraction. These size classes are outwardly similar to convergence clubs, and in fact confirmed the primary result of convergence club research which demonstrates that the divisions between rich and poor countries are the starkest and most clear-cut. However, the size classes I found are derived from theory that is a more appropriate fit to economic dynamics because it adequately incorporates realistic expectations of economies as complex adaptive systems. I argued that the underlying mechanisms, rather than emerging from conditions of initial equivalence, evolve and operate in multiple scale domains that

can be objectively identified and assessed, and suggested that understanding the patterns within and across scale domains may provide insight into the processes that structure wealth over time. This chapter also clearly demonstrated that transposing methods from one field to another has challenges, because while ecologies and economies are both complex adaptive systems, one is made up of multiple species and many well-defined processes, and the other is comprised largely of the human species with far more personal agency than non-humans, and many poorly-understood processes.

In Chapter 3, I tested whether socio-cultural-historical differences among countries could be responsible for structuring discontinuous size classes in cross-national GDP. The four variables I used (democracy, life expectancy, religion, and colonial status) have been proposed in the economics literature as likely playing a role in GDP, but have received far less attention than more typical econometrics. My results were equivocal, because while there were clear and persistent discontinuities in the datasets, they could not be attributed to the independent effect of each of the variables, and nor could those variables be ruled out as possible structuring processes. A secondary technique using an unsupervised ordination was able to more clearly demonstrate that countries that were similar to each other with regards to their variable classifications were more likely to cluster together in ordination space and belong to the same size class. In other words, countries that were Free (democratic standing), and Christian (religious standing) with a High Lifespan (life expectancy) clustered strongly compared to countries with other levels of those variables. The overall story mirrored that of Chapter 2, which is that the processes that occur in the tails of the data are more persistent and generate a stronger attractor than processes

structuring size classes in the middle of the distribution. It is also clear that to the extent that these socio-cultural variables structure economies, they do not operate in the same manner at all scales of the system, an outcome that is analytically challenging but also expected, given the hierarchical nature of scaling processes in other complex adaptive systems.

In Chapter 4, I applied the cross-scale resilience model to the coral reef fish communities of the Hawaiian archipelago, and tested the hypothesis that the cross-scale resilience structure of communities differed between the two regions of the archipelago (the less disturbed islands of the remote northern reaches of the archipelago, versus the habited islands of the southern part), or between coral-dominated and macro-dominated reef communities. Only within-scale redundancy had a significant effect on regimes within and across islands, and macro-turf communities expressed a higher within-scale redundancy, suggesting that the less desirable regime was also the more resilient.

In Chapter 5, I discussed a major limitation of the cross-scale resilience model as it currently stands, which is the absence of any consideration of abundance in either species or the functional roles they represent. I drew on an extensive ecological literature on abundance to detail the ways in which we would expect abundance to be relevant to the cross-scale resilience model, and put forward a series of testable hypotheses regarding the inclusion of abundance in the model. The primary message of this conceptual paper is that studies of two types are necessary to make a stronger mechanistic link between species and resilience as an emergent phenomena. First, we need to look for patterns in the distribution of abundance within and across scales, as pertains to species' functional roles. Although other researchers have looked at

patterns in abundance and functional diversity, no one does so in the context of the multi-scaled structure of ecosystems. Second, changes in the abundance of functions and the scales at which they occur are likely to provide strong signals of changing resilience and vulnerability to a regime shift, and this has value for researchers and managers.

In Chapter 6, I switched gears to focus on a concept that is a fundamental component of ecological resilience--the idea that complex systems self-organize to exist in regimes. Most work on regimes focuses on a single system changing regimes over time, but I focused on the idea of identifying regime boundaries across space using an information theory method that assesses order in data (Fisher Information). We used spatial data on zooplankton and avian communities to look for transitions between ecosystem types, and compared the results to the boundaries found in ecoregion maps such as those by Omernik and Bailey. The results made it clear that relying on traditional static ecoregion maps as the basis of boundary demarcation between ecosystem types was not appropriate given 1) the possibility of soft boundaries between ecosystems, 2) the non-stationary nature of vegetation and animal communities given climate change, and 3) the lack of correspondence between predicted community structure (as determined by the ecoregion maps) and observed community structure given land use changes. Comparing Fisher Information results to traditional early warning indicators and traditional multivariate analytical techniques also highlighted the added value that Fisher provided because of the explicit spatial information about community change absent from the other approaches. The results suggested that using Fisher information to track movement in

ecological boundaries over time could be a powerful methodology, given the current era of rapid and unpredictable ecological change.

And finally, in Chapter 7, I argued that the changing dynamics captured in the adaptive cycle are likely the result of endogenous processes inherent to complex adaptive systems, rather than just a handy conceptual metaphor. I drew on research from a wide range of scientific fields to support that claim, and then articulated the primary means by which the hypothesis could be tested in real systems. The most feasible approach for tracking system movement among the phases of the adaptive cycle is likely to be tracking changes in biomass. It is the most reasonable in its data requirements, and can be, with the development of already existing LiDAR technologies and the expansion of the discontinuity hypothesis to account for multiple taxa simultaneously, computable for both the floral and faunal components of ecological systems. Tracking changes in biomass within and across system scales would be, when combined with the cross-scale resilience model, a comprehensive and robust way to understand dynamics of change in complex systems and what those changes portend for the future structure and function of said system.

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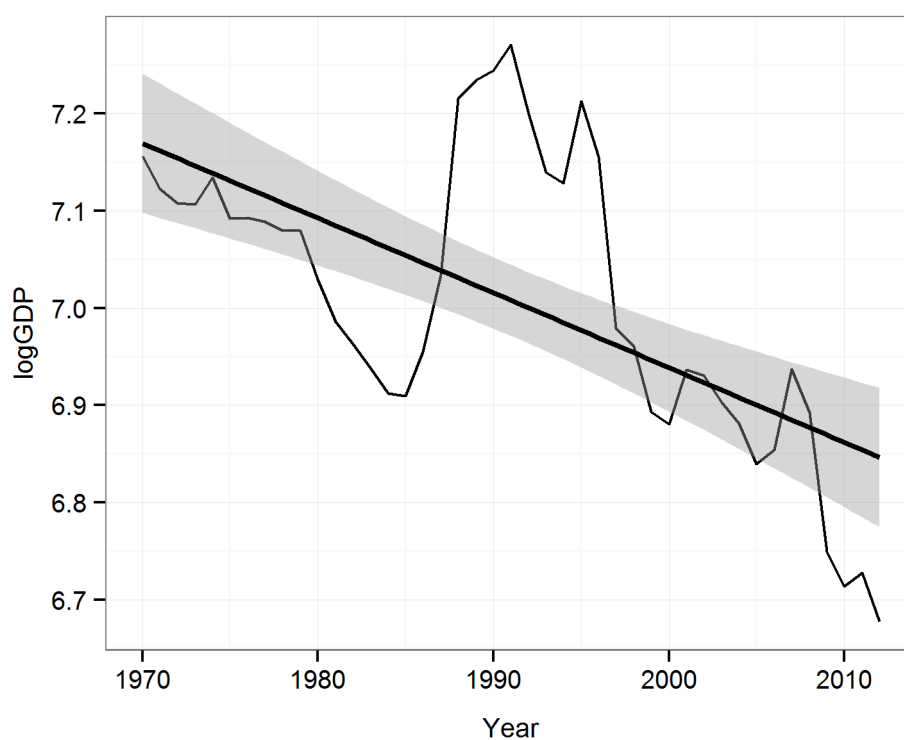
APPENDIX A DISCONTINUITIES IN CONSTANT GDP

Figure A.1 Change over time in the difference in wealth between the richest and poorest country.

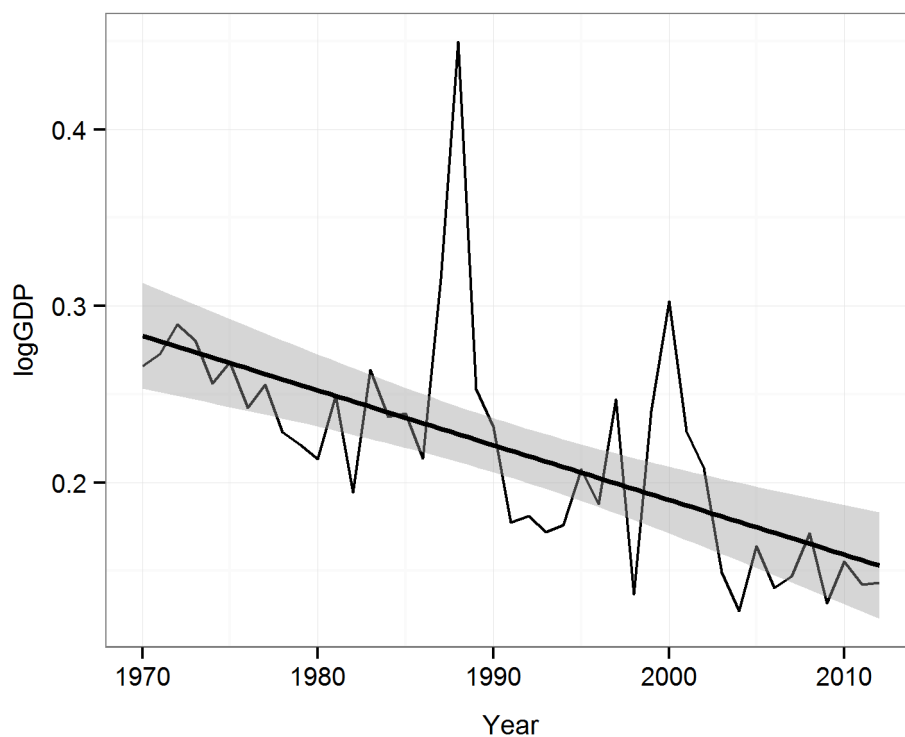


Figure A.2 Change in the average span of gaps.

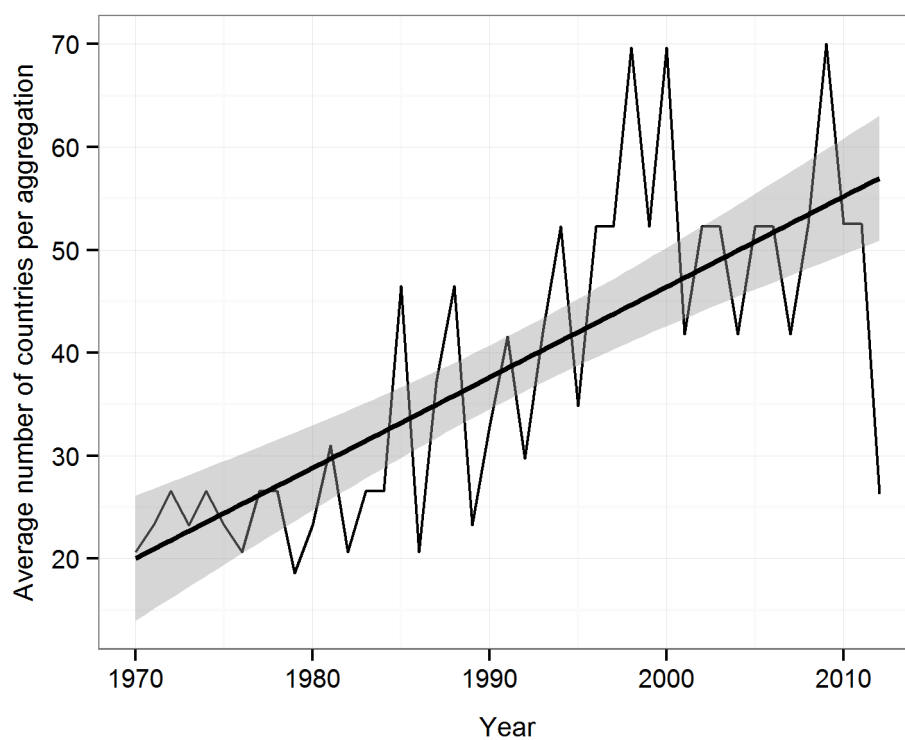


Figure A.3 Change in average number of countries per aggregation.

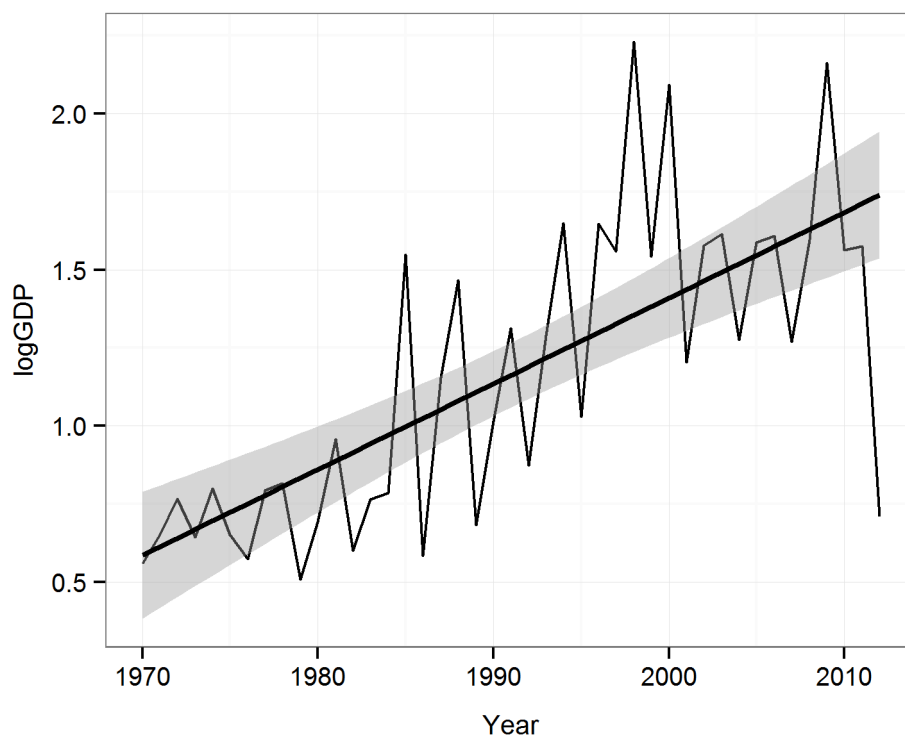


Figure A.4 Change in the average span of the aggregations.

Table 1 The frequency with which an annual distribution has a certain number of aggregation (43 years of data).

Number of aggregations	Frequency of occurrence
3	3
4	13
5	6
6	3
7	7
8	6
9	4
10	1

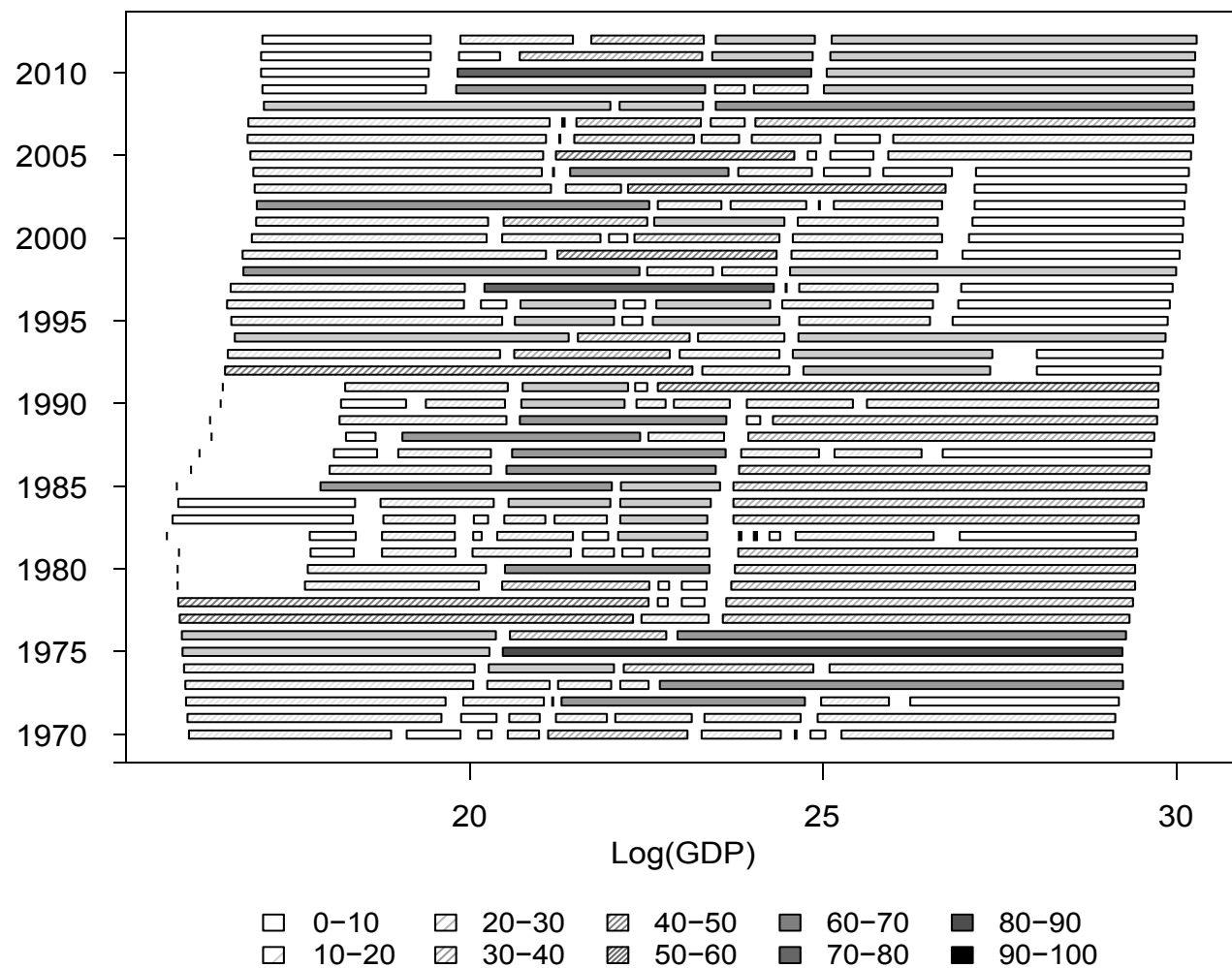


Figure A.5 Yearly discontinuous distribution of constant (2005) per capita GDP for 43 years. Shading represents the proportion of countries falling in each cluster. ([Figure 5 Appendix.pdf](#), 27kb)