

# UNLOCKING PATTERNS OF NATURE – THE MARRIAGE OF MATHEMATICS AND ECOLOGY

Cang Hui  
March 2015

*UNLOCKING PATTERNS OF NATURE – THE MARRIAGE OF MATHEMATICS AND ECOLOGY*

Inaugural lecture delivered on 19 March 2015

Prof Cang Hui  
Department of Mathematical Sciences  
Faculty of Science  
Stellenbosch University

Editor: SU Language Centre  
Printing: SUN MeDIA  
ISBN: 978-0-7972-1543-6  
Copyright © 2015 C Hui



## ABOUT THE AUTHOR

Cang Hui was born in the ancient capital of China, Xi'an, where the Terracotta Warriors were unearthed. In 1994, he went to Xi'an Jiaotong University, a C9 League, and obtained his BSc in applied mathematics four years later. He then moved to Lanzhou University and received his MSc in the same major in 2001 and a PhD in mathematical ecology in 2004. Immediately after his PhD, Hui came to South Africa and worked at Stellenbosch University until 2008 as a postdoctoral fellow in the Department of Conservation Ecology and Entomology. He was then appointed as a researcher by the DST-NRF Centre of Excellence for Invasion Biology (C-IB) in the Department of Botany and Zoology and worked there until the end of 2013. He was promoted to full professor in 2014 in the Department of Mathematical Sciences, which coincided with his appointment by

the NRF to the Tier I South African Research Chair (SARChI) in Mathematical and Theoretical Physical Biosciences, co-hosted by the African Institute for Mathematical Sciences (AIMS) in Cape Town.

Hui is working on the interface between mathematics and biology. His interests lie in proposing models and theories for explaining emerging patterns in whole-organism biology, namely ecology. Owing to their non-random nature, ecological processes are highly complex and adaptive. In order to quantify emergent ecological patterns and to investigate their hidden mechanisms, the simplicity of mathematical language is needed. His research focus is thus to develop novel, and apply available, methods in mathematics, statistics and theoretical physics for unlocking the mechanisms behind realistic biological patterns. More specifically, he examines how the heterogeneity of species distributions, the hierarchy of biological networks and the size of adaptive traits, change with measurement and organisational scales.

Hui is a P-rated researcher, a recipient of the 2011 Elsevier Young Scientist Award, a listed expert by the Mathematics of Planet Earth, a Chunhui Scholar, and adjunct professor at the Research School of Arid Environment and Climate Change at Lanzhou University. To date, he has published more than 100 scientific articles and serves on the editorial board of six international journals, among which *Biological Invasions*, *BMC Ecology*, and *Frontiers in Ecology and Evolution*. As a leading thinker in his field, he has been invited to deliver his perspectives on environmental sustainability at the Prince of Wales Seminar Series (Cambridge University Programme for Industry) and the Leaders Training Seminar (Mandela-Rhodes Foundation). Hui has successfully completed two NRF grants and is currently running another two NRF grants (SARChI and Incentive). He is also co-investigator of collaborative projects funded by the NRF, the National Science Foundation of China, National Geographic, CSIC (Spain), the Australian Research Council, and Groups on Earth Observations. Hui lives with his wife Beverley and daughter Keira in Cape Town.



# UNLOCKING PATTERNS OF NATURE – THE MARRIAGE OF MATHEMATICS AND ECOLOGY

Dedicated to Beverley and Keira

---

## I. INTRODUCTION

Nature never fails to amaze us. She reveals her beauty through things that we can quantify and measure, leaving those that are beyond our present intellectual grasp to the imagination. Scientific research endeavours to measure natural objects, to quantify patterns and structures from these measurements, and ultimately to identify the mechanisms governing these patterns and structures. This is equal to unveiling (i) what patterns exist in nature, (ii) how such patterns emerge, and (iii) why nature organises itself in such a way. Biological processes and structures are highly complex and adaptive. This means that natural patterns are contextual and contingent. The former denotes that the forms patterns take often change according to the circumstance and environment of the ecological system (there is no natural boundary or difficulty to generalise), while the latter indicates that different ecological elements together can achieve similar ecosystem function and evolutionary outcome (there are contingent past and future possibilities of an observed pattern). This has made some doubt the credibility of ecology as a 'hard' discipline of science.

Ecology studies the relationship between organisms and their environment, their interactions and functions, and finally the conservation and safeguarding of the function and service of ecosystems and the biosphere. It describes how species distribute and perform in response to environmental changes. Just like biological processes, ecological processes and structures are highly complex and adaptive. In order to quantify emerging ecological patterns and investigate their hidden mechanisms, we need to rely on the simplicity of mathematical language. It is an ideal system for further developing complexity science and systems thinking. Ecology, as a field of study, originated from natural history and soon developed into an experiment-based, hypothesis-testing science. In the past 20 years, a third wave has transformed, and is still transforming, this discipline. The four drivers of this third wave are the acceleration of computational power, mounting data from earth observation and molecular techniques, and the way knowledge is disseminated across the globe (Chave 2013). Ecology requires

mathematics (pure, applied and numerical) to become truly inter-, cross- and transdisciplinary and a flagship of complexity science.

## 2. ECOLOGICAL PATTERNS

Ecological patterns are emerging structures observed in populations, communities and ecosystems (Solé & Bascompte 2006; McCann 2012). Elucidating drivers behind ecological patterns can greatly improve our knowledge on how ecosystems assemble, function and respond to change and perturbation. The advent of access to large quantities of data, together with increased computing power, has led to a paradigm shift in ecology, away from manipulative experiments towards observation and pattern recognition (Sagarin & Pauchard 2012). This paradigm shift requires a closer marriage of quantitative and mathematical models, on the one hand, with observed or realised ecological complexity, on the other. Since 1992, when Levin (1992) raised the problem of pattern and scale as *the central problem in ecology and all natural sciences*, significant progress has been made in the field. Owing to their non-random nature, most, if not all, ecological patterns change with measurement and organisation scales, and exhibit distinct scaling properties. At present, a new suite of questions is being asked. It is necessary to capulate the knowledge gained so far on how to examine and interpret these scaling patterns in the language of mathematical models. This will stimulate the development of new quantitative approaches that are suitable for analysing and forecasting patterns of ecological systems.

The term 'scaling pattern' has been used on a wide range of occasions in ecology and basically denotes how observed metrics of the dynamics and structure of a focal system respond to changes in the dimension (i.e. support and scope) of that system. Indeed, nearly all ecological patterns are scale dependent. Such scale dependence creates both problems and opportunities for our inference, yet it also provides an avenue for us to examine the function and structure of especially complex systems, where manipulative experiments often become infeasible. It requires us to collect and sort a diverse array of scaling patterns in ecology, to summarise

mathematical models for examining and interpreting each scaling pattern, and finally to synthesise models of scaling patterns in a unified framework of multiscale modelling.

My research focuses on three specific areas: (i) cross-scale consistency in biodiversity patterns; (ii) from the parts to the whole in network emergence; and (iii) coupling ecological and evolutionary dynamics. When dealing with adjacent scales, we are in the realm of focus area (i). When the scales are quite different, often called different levels or hierarchies of complexity, we are dealing with focus areas (ii) and (iii). Using scale as a thread, these focus areas weave the kaleidoscope of ecological scaling patterns into a cohesive whole (Fig.1). In the remainder of this inaugural lecture, I give a brief introduction of these three research focuses, without resorting to their mathematical details (these can be examined by consulting the works cited).

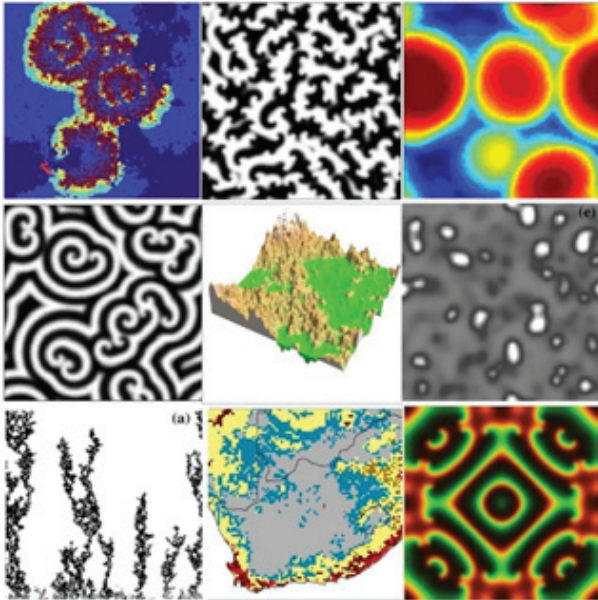


Fig.1: A list of self-emerging patterns collated from works by the Hui team largely using cellular automata.

## 2.1 Cross-scale consistency in biodiversity patterns

Ecological systems cover a range of scale that is relevant to humans and encompass the most diverse and striking phenomenon of life and its biodiversity (Fig.2). Models in this section deal with inferring patterns across scales that are in close proximity. As such, these models are often developed to ensure the consistency of measurements across different scales. To ensure the consistency, patterns across scales are usually bridged using probability theory. Specifically, this section presents

models that investigate how aggregated structures of organisms and biodiversity change with measurement scales; and which biological patterns resonate with underlying processes at the same characteristic scales, and why.

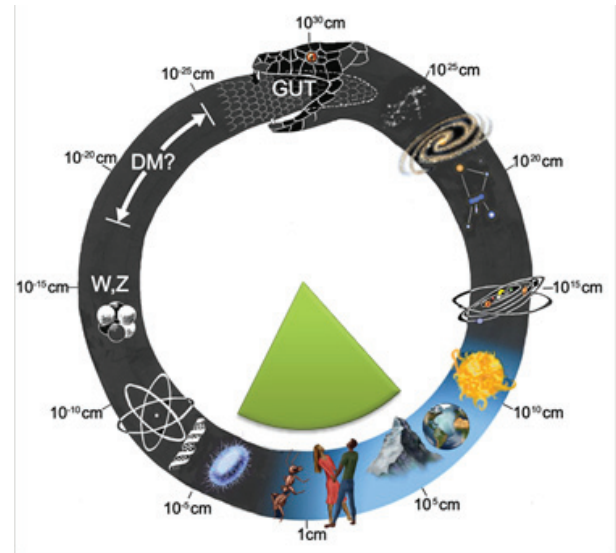


Fig.2: The Cosmic Uroboros of scales from the Planck scale to the cosmic horizon, with the scale of ecological processes covering the most interesting phenomenon of life and biodiversity. Image: Glashow's Snake rendered by Nancy Ellen Abrams and Joel R. Primack in 2006 (contributions to scalometer.wikispaces.com are licensed under a Creative Commons Attribution Share-Alike 3.0 License), with the green pie shape added by C. Hui.

Species distributions are not uniform across space, reflecting the interplay between habitat heterogeneity and the underlying nonlinear biotic regulation. When ecologists examine such non-random, aggregated patterns across scales, the Modifiable Areal Unit Problem presents itself (Fig.3; Openshaw 1984). The problem can be described as the change in species distribution characteristics as the grain and extent of sampling change (Wiens 1989; Jelinski & Wu 1996; Hui et al. 2010). There are ten, or more, models on the scaling pattern of occupancy, which depicts how species occupancy and its aggregation level change when scaled up or down (Azaele et al. 2012; Hanski & Gyllenberg 1997; He & Gaston 2000, 2003; He et al. 2002; Kunin 1998; Nachman 1981; Wright 1991; Zillio & He 2010) – including a Bayesian estimation model contributed by colleagues and myself (Hui et al. 2006; Hui 2009b). These models provide a universal basis for ensuring

cross-scale consistency. Under certain conditions, these models further allow researchers to extrapolate fine-scale occupancy and population densities from coarse-scale observations. Great potential exists to apply such predictive models in various cross-scale pattern analyses. As an aside: In 2014 Barwell et al. conducted a review of all existing models using an insect atlas of Britain, and the Hui model came out tops.

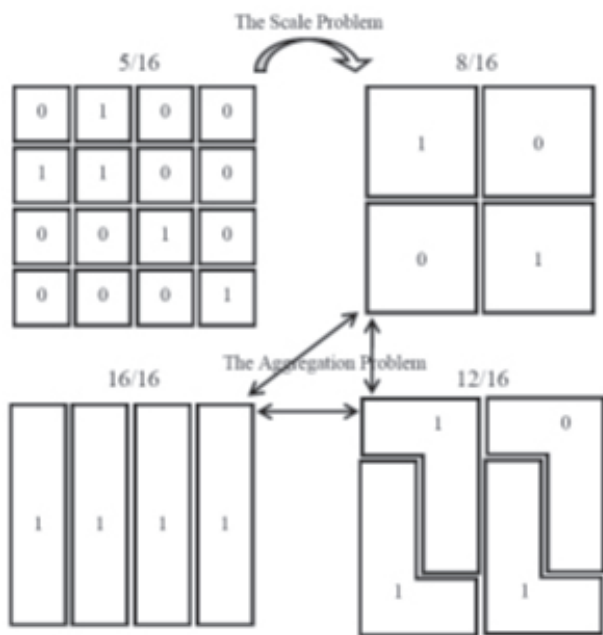


Fig.3: An illustration of the modifiable areal unit problem of merging four cells into a larger one but with different shapes (source: Hui 2009a).

The spatial and temporal scales of ecological processes are intertwined. Processes that account for the spatial distribution of species also underpin the temporal dynamics. This means that we can potentially forecast the future or rebuild history based solely on current spatial distribution, without resorting to long-term time series. Specifically, the scaling pattern of occupancy has been found to be related to population trends (Wilson et al. 2004; Borregaard & Rahbek 2006). As the ability to forecast the temporal trend of a focal species provides crucial information on its performance and viability, the methodology of *space-for-time substitution* is extremely appealing, especially since our ability to obtain spatial records has been drastically improved in recent years. We have developed a few models that can relate the scaling pattern of species occupancy to the near-future population trends (Hui 2011; Hui et al. 2012) and performance – in terms of the invasiveness of introduced species, for example (Hui et al. 2011, 2014). These models can be further expanded into an individual-based model, with non-stationary population

dynamics, to examine the overall relationship between the spatial and temporal patterns.

Just as two tuning forks of the same characteristic frequency resonate, so do ecological patterns and processes working on the same scale. For this I have coined the term *scale resonance*. For instance, species distributions are regulated by a variety of abiotic and biotic processes working in concert, but at different characteristic scales (McGill 2010; Peterson et al. 2011), whereas identified key processes (for example those using multivariate statistics) resonate with the measurement scale of the study (e.g. Roura-Pascual et al. 2011). That is, information being picked up is diluted by the measurement scale, rather than the intrinsic cross-scale mechanism. This finding brings into question many regional management planning practices that are based on the upscale extrapolation of local-scale studies (Guisan et al. 2013). We are aiming to explain the mechanism behind scale resonance in ecology and presenting a statistical remedy for cross-scale inference. This approach combines hierarchical partitioning (Chevan & Sutherland 1991; MacNally 1996) with the spatial autocorrelation – or distance decay of similarity (Nekola & White 1999) – of different ecological processes to depict how regression coefficients from the multivariate statistics change with spatial scales.

To exploit resources while mitigating conflicts, species often partition available habitats, forming co-distribution patterns of association or dissociation (Albrecht & Gotelli 2001). Null models based on permutation or niche-neutral processes have been widely applied for detecting signals of bio-interactions from *co-occurrence patterns* (Gotelli & Graves 1996; Gravel et al. 2006). However, co-occurrence is scale dependent (Bell 2005) and should be used with caution when inferring biotic interactions or processes. I have presented a probability model (Fig.4) based on the Bayesian principle that captures the transition from fine-scale dissociation to coarse-scale association in co-occurrence patterns (Hui 2009b). This can be further developed so that we can investigate how this change in co-occurrence patterns across scales affects our inference of the community assembly rule and its location on the niche-neutral continuum (Gravel et al. 2006).

Species diversity patterns, such as the species-area curve, endemics-area relationship, distance decay of similarity, and occupancy frequency distribution (e.g. Hui & McGeoch 2007a, b), reflect the scale-dependence of *species turnover* (Gaston & Blackburn 2000; Conlisk et al. 2007; McGlenn & Hurlbert 2012). Measures of spatial turnover in the compositional similarity or difference

between assemblages are commonly based on beta diversity, which was originally derived for pairwise comparisons of individual assemblages. However, none of the metrics of species turnover are able to fully reduce all diversity partitions in multiple-assemblage cases, meaning that the diversity components of three or more assemblages cannot be completely expressed using pairwise species turnover. Thus, pairwise metrics are not entirely adequate for depicting compositional similarity across multiple assemblages (Chao et al. 2008; Hui & McGeoch 2008; Baselga 2013). We have proposed a species turnover framework for diversity partitioning across multiple assemblages (Hui & McGeoch 2014), known as zeta diversity (Fig.5). Based on this new framework of multi-assemblage diversity partitioning, we can deduce commonly known diversity scaling patterns using the inclusion-exclusion principle, thereby making the connection between patterns, and elucidating how they change with scale.

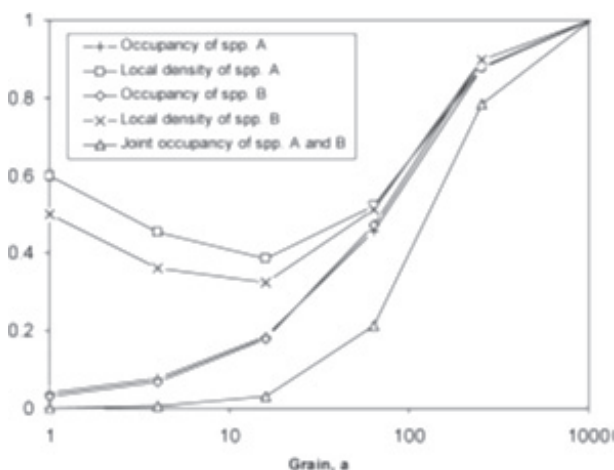


Fig.4: An illustration of the scaling pattern of occupancy and species association (source: Hui 2009b).

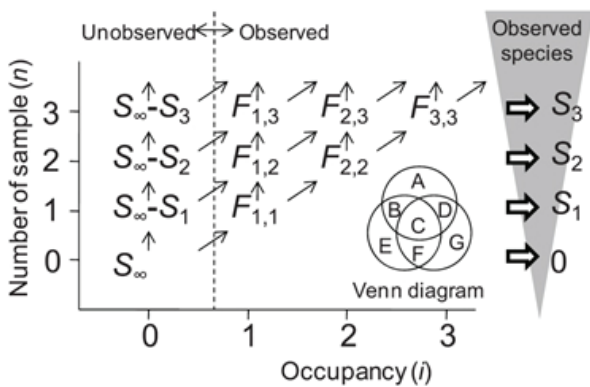


Fig.5: Zeta diversity, a new metric of species turnover, explained (source: Hui & McGeoch 2014).

## 2.2 From the parts to the whole in network emergence

When the gap between the two scales of interest is large enough, we are shifting from dealing with pattern inference across adjacent scales to connecting different hierarchical levels in a system. In particular, we are dealing with self-organised pattern emergence in bottom-up models of ecological networks. The function and architecture of ecological networks emerge from the life-history, physiological constraints and optimisation of each population in the network. Specifically, the scaling pattern of hierarchy depicts how the structure and function of asymmetrical ecological systems emerge and change with the system complexity. Using ecological networks as a proxy (Fig.6), we aim to investigate how cascade interactions affect the robustness and resilience of networks; how network architectures, especially nestedness and compartmentalisation, emerge and function; and what role network complexity plays in the stability of ecological networks.



Fig.6: A portrait of the food web. Engraving, Big fish eat little fish (1557) by Pieter van der Heyden, after Pieter Bruegel the Elder (Netherlandish, ca. 1525–1569).

Forty years ago, Robert May published his iconic book, *Stability and Complexity in Model Ecosystems*. Using a mathematical model of differential equations, May proposed a counterintuitive proposition to the commonly held belief in ecological circles that complexity leads to instability. The scientific endeavour to resolve May's complexity and stability dilemma by using networks as a proxy is a classic, ongoing example of how the characteristics of the parts affect the function of the whole in ecology. In the work my colleagues and I do, we follow on the complexity-stability debate in three aspects. First, we trace the progress made in the cascade model based on the Markov process on graphs (Cohen



& Newman 1985; Williams & Martinez 2000; Cattin et al. 2004; Minoarivelo et al. 2014). Second, we follow the development of hybrid models with increasingly complicated compositions and strengths of interactions (Allesina & Tang 2012; Mougi & Kondoh 2012; Neutel & Thorne 2014). Finally, we follow the development of models implementing adaptive foraging behaviours (Kondoh 2003; Suweis et al. 2013). Besides addressing the complexity-stability dilemma, these models further explain a wide range of network architectures, from node-degree distribution and productivity, to nestedness and modularity.

Mutualistic interactions are crucial processes to sustain ecosystem functions and services, foster biodiversity, and affect community stability (Bascompte & Jordano 2007; Okuyama & Holland 2008; Bastolla et al. 2009). Mutualistic networks often exhibit a distinctive nested structure, with the observed level of nestedness significantly higher than that of random networks generated by a variety of null models, yet still much lower than that of perfectly nested networks (Bascompte et al. 2003). It is evident that species often switch their interactive partners in real-world mutualistic networks, such as pollination and seed-dispersal networks, and this adaptive behaviour can be important to the structure and stability of networks (Valdovinos et al. 2010). We developed a novel model that incorporates an adaptive interaction switch (Zhang et al. 2011). The model has good predictive power, with 76.8% variance of nestedness explained in 81 empirical mutualistic networks. In contrast, a pure optimisation process of fitness gain constantly results in a perfectly nested network and thus completely exaggerates the level of nestedness in real networks. Instead, Alfred Russel Wallace's principle of natural selection via the elimination of the unfit, where a species can switch its interaction with the least contributing partner to a randomly selected new partner (that is: adaptive rule plus random drift), not only leads to a realistic level of nestedness, but also enhances the total abundance of individuals in the mutualistic network.

Antagonistic interactions, such as herbivory, parasitism and predation, are important to the provision of ecosystem functions and services (Dobson et al. 2008). It represents the process of resource exploitation in ecological networks (Van Alphen et al. 2003) and can divide species into clusters where consumers within a cluster are likely to share the same function and exploit similar resources (Guimera et al. 2010; Krasnov et al. 2012; Hui et al. 2013). Such a clustering architecture (Fig.7) – also known as compartmentalisation – can

have profound effects on the stability of ecological communities (Bascompte et al. 2006; Thebault & Fontaine 2010). Specifically, compartmentalisation tends to stabilise ecological networks by containing the effect of perturbations within modules (Stouffer & Bascompte 2011). Despite their important role in securing ecosystem functions and services during perturbations, mechanisms that can account for the level of compartmentalisation close to those observed in real ecological networks remain poorly understood. Although a number of models have been put forward to explain the emergence of functions and compartmentalisation in antagonistic networks, most can be criticised for their poor predictive power. A recent update on the optimal foraging theory by Zhang & Hui (2014) suggests that imprints from past experience and hunger aversion can make consumers prefer abundant resources to those that are rare even if the abundant resources are less profitable than the rare ones (Fig.8).

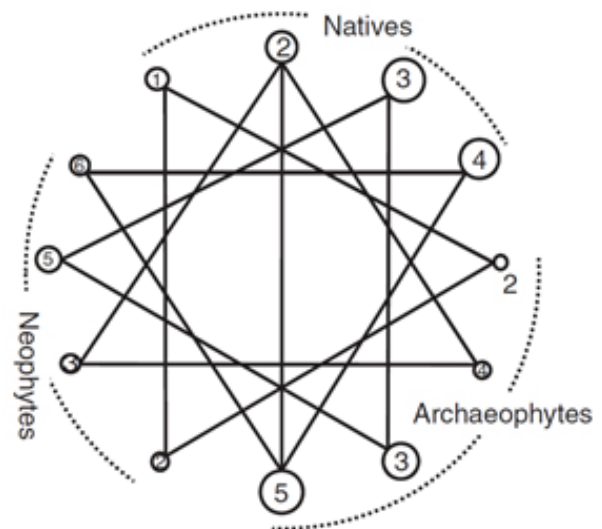


Fig.7: Geographical overlaps between modules of reserves, with a solid line indicating a substantial similarity (Jaccard's similarity  $J > 0.2$ ) (source: Hui et al. 2013).

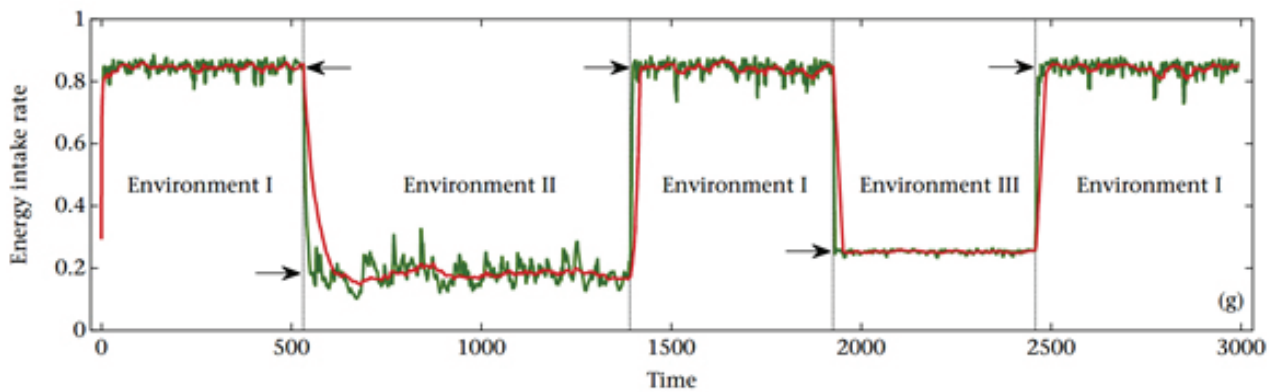


Fig.8: The recent experience driven (RED) strategy follows the optimal energy intake rate in changing environment (source: Zhang & Hui 2014).

At present, we are designing a hybrid behavioural rule which describes adaptive interaction switching and random drift and has been incorporated into a bipartite network model (Nuwagaba et al. 2015). The hybrid behavioural rule alone can explain the nearly 40% variation of observed modularity in 61 real networks. Together with network size and complexity, it can account for more than 90% of the variation of network modularity.

Allometric scaling is the most salient pattern demonstrating how biological rates, especially metabolic rate, are regulated by organism size. Models based on constraints in the cardiovascular and respiratory transportation networks for multicellular organisms have yielded a simple explanation to the  $\frac{3}{4}$  power law of metabolic scaling (West et al. 1997, 1999; Banavar et al. 1999, 2014). This has led to a number of developments related to connecting body size to patterns of biodiversity and networks (Banavar et al. 2002; Ritchie & Olff 1999; West et al. 2001; Allen et al. 2002; Enquist & Niklas 2001; Woodward et al. 2005; White et al. 2007). Our ultimate goal is to develop a cross-scale model that connects body size to metabolism, ontogeny, recruitment, abundance, distribution, biodiversity, and ecological networks. This model could borrow insights from other models, such as that proposed by Loeuille and Loreau (2005) and scales up individual metabolism to ecosystem patterns via adaptive interaction strengths caused through evolving body size (Brännström et al. 2011).

### 2.3 Coupling ecological and evolutionary scales

**E**cological patterns not only emerge from scales and hierarchies, but also from the coupling of fast and slow processes. This section presents the most obvious

examples of coupling fast and slow processes, namely coupling processes operating on ecological (fast) and evolutionary (slow) scales. Work done during the last few decades as well as recent developments in models have allowed us to deal with the coupling of ecological and evolutionary scales under the banner of frequency-dependent selection. Models in this section are designed to bridge any gaps that may exist when working with the concurrency of ecological and evolutionary processes.

Evolutionary dynamics concern a few key variables: genotypes and traits of interest; the relative abundance (frequency) of specific traits; the fitness of the genotype which is defined as its replication rate and dependent on both its trait value and frequency; and finally the mutation rate. Several models are available that depict the interplay of these variables: the quasi-species equation of molecular evolution, evolutionary game theory, the replicator-mutation equation, the Price equation, adaptive dynamics, and a few unified models that synthesize all these specific models into one (e.g. Page & Nowak 2002; Champagnat et al. 2006). A standard procedure for analysing these models is known as the evolutionary invasion analysis (Otto & Day 2007), where the evolutionary singularity and selection gradient are examined with the faster ecological dynamics set at its equilibrium (Dieckmann & Doebeli 1999; Dieckmann et al. 2004). Together, these models and their unified forms provide a complete description of evolutionary dynamics and behaviour under natural selection. It is time to synthesise these mathematical models of trait evolution. In particular, my colleagues and I pay attention to the use of evolutionary invasion analysis for analysing such ecological and evolutionary feedbacks in frequency-dependent selection. We further present a unifying model to include mutation correlation between traits, shape of fitness landscape, intraspecific frequency-

dependent selection, and interspecific frequency-dependent selection or coevolution (Fig.9). We examine the conditions for evolutionary branching and traps – which is of particular interest to those involved in biodiversity maintenance (Dercole & Rinaldi 2008; Leimar 2009; Zhang et al. 2013), as depicted in Fig.10, – as well as the direction and speed of evolutionary branching in multidimensional systems (i.e. multiple species with multiple traits).



Fig.9: Coevolution is exemplified by the interaction between the long-proboscid fly, *Moegistorhynchus longirostris*, and the long-tubed iris, *Lapeirousia anceps*, in South Africa. Photo courtesy: A. Pauw.

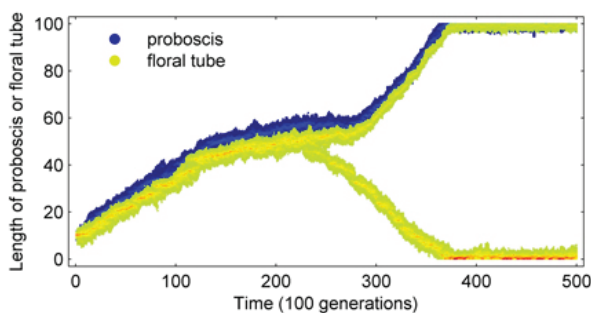


Fig.10: Individual-based simulations of the coevolution between fly proboscis and floral tube (source: Zhang et al. 2014).

Research into the impact of evolution by using contemporary scales, also known as rapid eco-evolutionary feedback, has gained momentum in the literature, especially when dealing with adaptive response to global changes (Schoener et al. 2011; Agrawal et al. 2012; Berthouly-Salazar et al. 2013). This kind of rapid evolution challenges the standard approach, in which the fast ecological dynamics are set at equilibrium during the analysis, and calls for further consideration of the impact created by the dynamic behaviours of both traits and populations (Ellner et al. 2011; Zhang & Hui 2011; Becks et al. 2012). Currently, we are examining a few models of rapid evolution. First, from McLaughlin and Roughgarden (1993) to Hairston et al. (2005), a few models have been developed to allow the examination of species interactions at different paces. Second, models of adaptive dynamics have been developed to deal with continuous trait distributions (Diekmann et al. 2005; Perthame & Cauduchon 2010; Doebeli & Ispolatov 2010). These models bridge any gaps that may exist given the concurrency of ecological interactions and evolutionary adaptation, providing a platform for examining the intertwined eco-evolutionary dynamics.

### 3. SYNTHESIS: ADVICE FROM A CATERPILLAR

We are on an interesting journey of examining ecological systems on different spatial and temporal scales. As our first research focus, we infer biodiversity patterns across scales. As our second focus, we assemble the function of a whole network from the parts. As our third focus, we connect the fast ecological pace with the slow evolutionary one. These three research areas all serve to clarify the interactions among patterns, scales and dynamics in the ever-evolving ecological system. This means that natural patterns are contextual and contingent, and ecological systems can be the heart of the transdisciplinary third wave of research. A perfect marriage of mathematics and ecology can lead the way.

At this stage the audience may be feeling a little giddy and uncomfortable – not unlike Alice in Wonderland. “[B]eing so many different sizes in a day is very confusing”, she complains. “It isn’t,” replies the Caterpillar of the absurd world. Alice, not one to give up easily, puts her case. “Well, [...] when you have to turn into a chrysalis [...] and then after that into a butterfly, I should think you’ll feel it a little queer, won’t you?” “Not a bit,” retorts the Caterpillar.

Indeed, changing and coupling scales has become the new norm in ecology. The advice from the Caterpillar to Alice is, “Keep your temper”, “You’ll get used to it in time”, and “One side [of the mushroom] will make you grow taller, and the other side will make you grow shorter”. Throughout the endeavour, we build models to retain cross-scale consistency and find bridges to connect processes examining the parts to those investigating the whole, or fast with slow. Mutation, drift, selection and migration are the four forces of evolution. These forces have led to species interactions and distributions at different scales in a multiplayer game of chance and individual fitness gain. As processes are intertwined in space and time, the signal of adaptation through individual fitness gain at this ‘Red Queen’s feast’ will be lost when moving away from the relevant scales. Cross-scale consistency and the connection of concurrent processes are the contained ‘temper’ to make sense of the ‘Wonderland’ of ecology and the wizardliness of mathematics.

Gerhard and Jane Laniewski, and Bev and Keira for their patience and loyalty through ups and downs. Nothing is possible without the support of my research by the NRF, the NSFC, National Geographic, the CSIC, the ARC and GEO BON, as well as the support of the DST-NRF Centre of Excellence for Invasion Biology, the African Institute for Mathematical Sciences, and Stellenbosch University.

## ACKNOWLEDGEMENTS

I am grateful for the mentorship of Melodie McGeoch, Dave Richardson, Zi-zhen Li and Zhi-en Ma in my academic career so far, and for the encouragement and ideas from Steven Chown, Kevin Gaston, Ulf Dieckmann, Jessica Gurevitch, Lev Ginzburg, Gordon Fox, Jane Molofsky, Marie-Josée Fortin, Joe Miller, Yoh Iwasa, Bill Kunin, Sandy Liebhold, Petr Pyšek, Tim Blackburn, Anne Magurran, Jeff Sanders, Mike Samways, Guozhen Du, Brian van Wigen, Bruce Maxwell, Bai-lian (Larry) Li and Fangliang He, Mirijam Gartner, Barry Green, Ingrid Rewitzky, Jeff Sanders, Sarah Davies, Nuria Roura-Pascual, Luz Boyero, Karl Evans, Lluís Brotons, Åke Brännström, John Terblanche, Jaco le Roux, Bettine van Vurren, Llewellyn Foxcroft, Rainer Krugs, John Wilson, Olaf Weyl, Pete le Roux, Ruan Veldtman, Helen de Klerk, Zahn Munich, Sophie von der Heyden, Susana Clusella-Trullas, Anton Pauw, Karen Esler, Alison Leslie, Sonja Matthew, Michael Samways, Anibal Pauchard, Martin Nunez, Arnost Sizling, Mathew Rouget, Mark Robertson, Berndt van Rensburg, Belinda Reyers, Nigel Andrew, Paul Caplat, Tobias Plieninger, Cécile Berthouly-Salazer, Denise Mager, Darragh Woodford, Linke Potgieter, Farai Nyabadza, Jakub Horak, Terence Jayiya, Zihua Zhao, Peijian Shi, Min Su, Xiaozhuo Han, Feng Zhang, Dongxia Yue, and many young talented persons and visitors who have passed through my lab. I am grateful also to a number of friends, Ulli and Heide Leihman, Helen de Villiers, and families, Jun Hui and Shufang Xing,

## REFERENCES

- Agrawal, A.A., Hastings, A.P., Johnson, M.T., Maron, J.L. & Salminen, J.-P. (2012) Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science*, 338: 113-116.
- Albrecht, M. & Gotelli, N.J. (2001) Spatial and temporal niche partitioning in grassland ants. *Oecologia*, 126: 134-141.
- Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297: 1545-1548.
- Allesina, S. & Tang, S. (2012) Stability criteria for complex ecosystems. *Nature*, 483: 205-208.
- Azaele, S., Cornell, S.J. & Kunin, W.E. (2012) Downscaling species occupancy from coarse spatial scales. *Ecol. Appl.*, 22: 1004-1014.
- Banavar, J.R., Cooke, T.J., Rinaldo, A. & Maritan, A. (2014) Form, function, and evolution of living organisms. *Proc. Natl. Acad. Sci. USA*, 111: 3332-3337.
- Banavar, J.R., Damuth, J., Maritan, A. & Rinaldo, A. (2002) Modelling universality and scaling. *Nature*, 420: 626-627.
- Banavar, J.R., Maritan, A. & Rinaldo, A. (1999) Size and form in efficient transportation networks. *Science*, 399: 130-132.
- Barwell, L., Isaac, N.J.B. & Kunin, W.E. (2014) Can coarse-grain patterns in insect atlas data predict fine-grain occupancy? *Divers. Distrib.*, 20: 895-907.
- Bascompte, J. & Jordano, P. (2007) Plant–animal mutualistic networks: The architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 38: 567-593.
- Bascompte, J., Jordano, P. & Olesen, J.M. (2006) Asymmetric coevolution networks facilitate biodiversity maintenance. *Science*, 312: 431-433.
- Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA*, 100, 9383-9387.
- Baselga, A. (2013) Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, 36: 124-128.
- Bastolla, U., Fortuna, M.A., Pascual-Garcia, A., Ferrera, A., Luque, B. & Bascompte, J. (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, 458: 1018-1020.
- Becks, L., Ellner, S.P., Jones, L.E. & Hairston, N.G. (2012) The functional genomics of an eco-evolutionary feedback loop: Linking gene expression, trait evolution, and community dynamics. *Ecol. Lett.*, 15: 492-501.
- Bell, G. (2005) The co-distribution of species in relation to the neutral theory of community ecology. *Ecology*, 86: 1757-1770.
- Berthouly-Salazar, C., Hui, C., Blackburn, T.M., Gaboriaud, C., Van Rensburg, B.J., Van Vuuren, B.J. & Le Roux, J.J. (2013) Long-distance dispersal maximizes evolutionary potential during rapid geographic range expansion. *Mol. Ecol.*, 22: 5793-5804.
- Borregaard, M.K. & Rahbek, C. (2006) Prevalence of intraspecific relationship between range size and abundance in Danish birds. *Divers. Distrib.*, 12: 417-422.
- Brännström, A., Loeuille, N., Loreau, M. & Dieckmann, U. (2011) Emergence and maintenance of bio-diversity in an evolutionary food-web model. *Theor. Ecol.*, 4: 467-478.
- Cattin, M.-F., Bersier, L.-F., Banasek-Richter, C., Baltensperger, M. & Gabriel, J.-P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427: 835-839.
- Champagnat, N., Ferriere, R. & Meleard, S. (2006) Unifying evolutionary dynamics: From individual stochastic processes to macroscopic models. *Theor. Popul. Biol.*, 69: 297-321.
- Chao, A., Jost, L., Chiang, S.C., Jiang, Y.H. & Chazdon, R.L. (2008) A two-stage probabilistic approach to multiple-community similarity indices. *Biometrics*, 64: 1178-1186.
- Chave, J. (2013) The problem of pattern and scale in ecology: What have we learned in 20 years? *Ecol. Lett.*, 16: 4-16.
- Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *Am. Stat.*, 45: 90-96.
- Cohen, J.E. & Newman, C.M. (1985) A stochastic theory of community food webs: I. Models and aggregated data. *Proc. R. Soc. B*, 224: 421-448.
- Conlisk, E., Bloxham, M., Conlisk, J., Enquist, B. & Harte, J. (2007) A new class of models of spatial distribution. *Ecol. Monogr.*, 77: 269-284.
- Dercole, F. & Rinaldi, S. (2008) Analysis of evolutionary processes: The adaptive dynamics approach and its applications. Princeton University Press.

- Dieckmann, U. & Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature*, 400: 354-357.
- Dieckmann, U., Doebeli, M., Metz, J.A.J. & Tautz, D. (eds.) (2004) Adaptive speciation. Cambridge University Press.
- Dieckmann, O., Jabin, P.-E., Mischler, S. & Perthame, B. (2005) The dynamics of adaptation: An illuminating example and a Hamilton-Jacobi approach. *Theor. Popul. Biol.*, 67: 257-271.
- Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F. & Jetz, W. (2008) Homage to Linnaeus: How many parasites? How many hosts? *Proc. Natl. Acad. Sci. USA*, 105: 11482-11489.
- Doebeli, M. & Ispolatov, I. (2010) Complexity and diversity. *Science*, 328: 494-497.
- Ellner, S.P., Geber, M.A. & Hairston, N.G. (2011) Does rapid evolution matter? Measuring the rate of contemporaneous evolution and its impacts on ecological dynamics. *Ecol. Lett.*, 14: 603-614.
- Enquist, B.J. & Niklas, K.J. (2001) Invariant scaling relations across tree-dominated communities. *Nature*, 410: 655-660.
- Gaston, K.J. & Blackburn, T.M. (2000) Pattern and process in macroecology. Blackwell Science.
- Gotelli, N.J. & Graves, G.R. (1996) Null models in ecology. Smithsonian Institution Press.
- Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006) Reconciling niche and neutrality: The continuum hypothesis. *Ecol. Lett.*, 9: 399-409.
- Guimera, R., Stouffer, D.B., Sales-Pardo, M., Leicht, E.A., Newman, M.E.J. & Amaral, L.A.N. (2010) Origin of compartmentalisation in food webs. *Ecology*, 91: 2941-2951.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.P., Possingham, H.P. & Buckley, Y.M. (2013) Predicting species distributions for conservation decisions. *Ecol. Lett.*, 16: 1424-1435.
- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.*, 8: 1114-1127.
- Hanski, I. & Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, 284: 397-400.
- He, F. & Gaston, K.J. (2000) Estimating species abundance from occurrence. *Am. Nat.*, 156: 553-559.
- Hui, C. (2009a) A Bayesian solution to the modifiable areal unit problem. In: Hassani, A.-E., Abraham, A. & Herrera, F. (eds.) *Foundations of Computational Intelligence Volume 2: Approximate Reasoning*, pp. 175-196. Springer.
- Hui, C. (2009b) On the scaling pattern of species spatial distribution and association. *J. Theor. Biol.*, 261: 481-487.
- Hui, C. (2011) Forecasting population trend from the scaling pattern of occupancy. *Ecol. Model.*, 222: 442-446.
- Hui, C. & McGeoch, M.A. (2007a) A self-similarity model for occupancy frequency distribution. *Theor. Popul. Biol.*, 71: 61-70.
- Hui, C. & McGeoch, M.A. (2007b) Modeling species distributions by breaking the assumption of self-similarity. *Oikos*, 116: 2097-2107.
- Hui, C. & McGeoch, M.A. (2008) Does the self-similar species distribution model lead to unrealistic predictions? *Ecology*, 89: 2946-2952.
- Hui, C. & McGeoch, M.A. (2014) Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns. *Am. Nat.*, 184: 684-694.
- Hui, C., Richardson, D.M., Pyšek, P., Le Roux, J.J., Kučera, T. & Jarošík, V. (2013) Increasing functional modularity with residence time in the co-distribution of native and introduced vascular plants. *Nat. Commun.*, 4: 2454.
- Hui, C., Boonzaaijer, C. & Boyero, L. (2012) Estimating changes in species abundance from occupancy and aggregation. *Basic Appl. Ecol.*, 13: 169-177.
- Hui, C., McGeoch, M.A. & Warren, M. (2006) A spatially explicit approach to estimating species occupancy and spatial correlation. *J. Anim. Ecol.*, 75: 140-147.
- Hui, C., McGeoch, M.A., Reyers, B., Le Roux, P.C., Greve, M. & Chown, S.L. (2009) Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecol. Appl.*, 19: 2038-2048.
- Hui, C., Richardson, D.M., Robertson, M.P., Wilson, J.R.U. & Yates, C.J. (2011) Macroecology meets invasion ecology: Linking the native distributions of Australian acacias to invasiveness. *Divers. Distrib.*, 17: 872-883.
- Hui, C., Richardson, D.M., Visser, V. & Wilson, J.R.U. (2014) Macroecology meets invasion ecology: Performance of Australian acacias and eucalypts around the world foretold by features of their native ranges. *Biol. Invas.*, 16: 565-576.
- Hui, C., Veldtman, R. & McGeoch, M.A. (2010) Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography*, 33: 95-102.

- Kondoh, M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299: 1388-1391.
- Krasnov, B.R., Fortuna, M.A., Mouillot, D., Khokhlova, I.S., Shenbrot, G.I. & Poulin, R. (2012) Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *Am. Nat.*, 179: 501-511.
- Kunin, W.E. (1998) Extrapolating species abundance across spatial scales. *Science*, 281: 1513-1515.
- Leimar, O. (2009) Multidimensional convergence stability. *Evol. Ecol. Res.*, 11:191-208.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, 73: 1943-1967.
- Loeuille, N. & Loreau, M. (2005) Evolutionary emergence of size-structured food webs. *Proc. Natl. Acad. Sci. USA*, 102: 5761-5766.
- MacNally, R. (1996) Hierarchical partitioning as an interpretative tool in multivariate inference. *Aust. J. Ecol.*, 21: 224-228.
- McCann, K.S. (2012) *Food webs*. Princeton University Press.
- McGill, B.J. (2010) Matters of scale. *Science*, 3288: 576.
- McGlinn, D. & Hurlbert, A.H. (2012) Scale dependence in species turnover reflects variance in species occupancy. *Ecology*, 93: 294-302.
- McLaughlin, J. & Roughgarden J. (1993) Species interactions in space. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (ed.) R.E. Ricklefs & D. Schluter, pp.89-98, University of Chicago Press.
- Minoarivelo, H.O., Hui, C., Terblanche, J.S., Kosakovsky Pond, S.L. & Scheffler, K. (2014) Detecting phylogenetic signal in mutualistic interaction networks using a Markov process model. *Oikos*, 123: 1250-1260.
- Mougi, A. & Kondoh, M. (2012) Diversity of interaction types and ecological community stability. *Science*, 337: 349-351.
- Nachman, G. (1981) A mathematical model of the functional relationship between density and spatial distribution of a population. *J. Anim. Ecol.*, 50: 453-460.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *J. Biogeogr.*, 26: 867-878.
- Neutel, A.-M. & Thorne, M.A.S. (2014) Interaction strengths in balanced carbon cycles and the absence of a relation between ecosystem complexity and stability. *Ecol. Lett.*, 17: 651-661.
- Nuwagaba, S., Zhang, F. & Hui, C. (2015) A hybrid behavioural rule of adaptation and drift explains the emergence of compartmentalization in antagonistic networks. *Proc. R. Soc. B*, under review.
- Okuyama, T. & Holland, J.N. (2008) Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.*, 11: 208-216.
- Openshaw, S. (1984) *The modifiable areal unit problem*. GeoBooks.
- Otto, S.P. & Day, T. (2007) *A biologist's guide to mathematical modelling in ecology and evolution*. Princeton University Press.
- Page, K.M. & Nowak, M.A. (2002) Unifying evolutionary dynamics. *J. Theor. Biol.*, 219: 93-98.
- Perthame, B. & Cauduchon, M. (2010) Survival thresholds and mortality rates in adaptive dynamics: Conciliating deterministic and stochastic simulations. *Math. Med. Biol.*, 27: 195-210.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araujo, M.B. (2011). *Ecological niches and geographic distributions*. Princeton University Press.
- Ritchie, M.E. & Olff, H. (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, 400: 557-560.
- Roura-Pascual, N., Hui, C., Ikeda, T., Leday, G., Richardson, D.M., Carpintero, S., Espadaler, X., Gómez, C., Guénard, B., Hartley, S., Krushelnycky, P., Lester, P.J., McGeoch, M.A., Menke, S.B., Pedersen, J.S., Pitt, J.P., Reyes, J., Sanders, N.J., Suarez, A.V., Touyama, Y., Ward, D., Ward, P.S. & Worner, S.P. (2011) Relative roles of climatic suitability and anthropogenic influence in determining the pattern of spread in a global invader. *Proc. Natl. Acad. Sci. USA*, 108: 220-225.
- Sagarin, R. & Pauchard, A. (2012) *Observation and ecology: Broadening the scope of science to understand a complex world*. Island Press.
- Schoener, T.W. (2011) The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. *Science*, 331: 426-429.
- Solé, R.V. & Bascompte, J. (2006) *Self-organization in complex ecosystems*. Princeton University Press.

- Stouffer, D.B. & Bascompte, J. (2011). Compartmentalisation increases food-web persistence. *Proc. Natl. Acad. Sci. USA*, 108: 3648-3652.
- Suweis, S., Simini, F., Banavar, J.R. & Maritan, A. (2013) Emergence of structural and dynamical properties of ecological mutualistic networks. *Nature*, 500: 449-452.
- Thebault, E. & Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329: 853-856.
- Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narvaez, L., Urbani, P. & Dunne, J.A. (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol. Lett.*, 13: 1546-1559.
- Van Alphen, J.J.M., Bernstein, C. & Driessen, G. (2003) Information acquisition and time allocation in insect parasitoids. *Trends Ecol. Evol.*, 18: 81-87.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the structure and allometric scaling laws in biology. *Science*, 276: 122-126.
- West, G.B., Brown, J.H. & Enquist, B.J. (1999) The fourth dimension of life: Fractal geometry and Allometric scaling of organisms. *Science*, 284: 1677-1679.
- West, G.B., Brown, J.H. & Enquist, B.J. (2001) A general model for ontogenetic growth. *Nature*, 413: 628-631.
- White, E.P., Morgan Ernest, S.K., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends Ecol. Evol.*, 22: 323-330.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Funct. Ecol.*, 3: 385-397.
- Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*, 404: 180-183.
- Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*, 432: 393-396.
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends Ecol. Evol.*, 20: 402-409.
- Wright, D.H. (1991) Correlations between incidence and abundance are expected by chance. *J. Biogeogr.*, 1: 463-466.
- Zhang, F. & Hui, C. (2011) Eco-evolutionary feedback and the invasion of cooperation in prisoner's dilemma games. *PLoS ONE*, 6: e27523.
- Zhang, F. & Hui, C. (2014) Recent experience-driven behaviour optimizes foraging. *Anim. Behav.*, 88: 13-19.
- Zhang, F., Hui, C. & Pauw, A. (2013) Adaptive divergence in Darwin's race: How coevolution can generate trait diversity in a pollination system. *Evolution*, 67: 548-560.
- Zhang, F., Hui, C. & Terblanche, J.S. (2011) An interaction switch predicts the nested architecture of mutualistic networks. *Ecol. Lett.*, 14: 797-803.
- Zillio, T. & He, F. (2010) Modeling spatial aggregation of finite populations. *Ecology*, 91: 3698-3706.