

REVIEW AND SYNTHESIS

The problem of pattern and scale in ecology: what have we learned in 20 years?

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Abstract

Over the past 20 years, major advances have clarified how ecological patterns inform theory, and how in turn theory informs applied ecology. Also, there has been an increased recognition that the problem of scale at which ecological processes should be considered is critical if we are to produce general predictions. Ecological dynamics is always stochastic at small scales, but variability is conditional on the scale of description. The radical changes in the scope and aims of ecology over the past decades reflect in part the need to address pressing societal issues of environmental change. Technological advances in molecular biology, global positioning, sensing instrumentation and computational power should not be overlooked as an explanation for these radical changes. However, I argue that conceptual unification across ecology, genetics, evolution and physiology has fostered even more fertile questions. We are moving away from the view that evolution is played in a fixed ecological theatre: the theatre is being rapidly and relentlessly redesigned by the players themselves. The maintenance of ecosystem functions depends on shifts in species assemblages and on cellular metabolism, not only on flows of energy and matter. These findings have far reaching implications for our understanding of how ecosystem function and biodiversity will withstand (or not) environmental changes in the 21st century.

Keywords

Eco-evolutionary dynamics, global change, modularity, pattern, scale, spatial ecology.

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INTRODUCTION

Pattern implies some sort of repetition, and the existence of repetition implies that some prediction is possible (MacArthur 1972). Few research articles have been more influential to our discipline than Simon Levin's (1992) paper 'On the problem of pattern and scale in ecology'. It has introduced a generation of ecologists to interdisciplinary thinking, and to two crucial concepts for ecology, pattern and scale. He has also promoted the view that ecological processes act at a variety of spatial and temporal scales, and they generate patterns at scales that may differ from that at which processes act. To understand a system, it is important to study it at the appropriate scale, and develop models that bridge across scales. Twenty years after the publication of Levin (1992), and 40 years after that of MacArthur's (1972) 'Geographical Ecology', I took this opportunity to place the themes of this special issue in a historical perspective with the key concepts of pattern and scale, and ask how this recent history may hopefully help us to connect processes with pattern and scale to set a path forward in ecology.

Since 1992, ecology has witnessed and has been an actor of four major technological revolutions. The first and foremost revolution is the advent of the numeric era. Moore's law of the doubling capacity of computers every 2 years has been outpaced: over the past two decades, computer power has doubled every year. The computer on which this manuscript was typeset is one million times faster than the one I was trained on as a student 20 years ago. This has had innumerable consequences on the way we do science. Questions that pertained to the realm of speculation have been revisited, such as bioinformatics projects in molecular biology, some

of which are described below. The second revolution has been biochemical. New techniques of molecular biology, notably the polymerase chain reaction, have percolated into ecology labs and have thrived to a degree that was initially difficult to imagine. The journal *Molecular Ecology*, now one of the foremost outlets in ecology, was launched in 1992. High-throughput sequencing techniques are promising to transform again our research field. The third revolution has concerned environmental sensing. The seeds of change were already present in the 1980s, with the development of landscape ecology. Yet, reliable technology to develop research programs in global ecology. Transformative techniques such as Light detection and Ranging (LiDAR) or hyperspectral techniques have offered new ways to look at the Earth system. Of course, many more sensors have been implemented for ground-based applications, to measure fluxes or environmental variables (Vargas *et al.* 2010), to follow the spatial movement of individuals or to record their behaviour, (Katz *et al.* 2011). The fourth and last revolution relates to our ability today to disseminate information and knowledge at a global scale, with far-ranging consequences on our ability to develop collaborative science among researchers but also foster the development of a vast knowledge base in natural history, with contributions from concerned citizen (Silvertown 2009).

Central issues of ecology have also shifted significantly over the past two decades. Global environmental changes have been an overwhelming factor of change. For instance, the human population has increased by 25% and fossil CO₂ emissions by 40% (Le Quéré *et al.* 2009). Most models suggest that this should result in a doubling in radiative forcing by 2050 (Moss *et al.* 2010). These trends have been accompanied by a regional shift of traditional foci of environmental

concern. The 20th anniversary of the Rio Earth Summit has been the occasion to confirm that the goals of reducing the threats to biological diversity have not been met today. If anything, things have gotten worse.

Understanding the translation of dynamics across scales in ecosystems, and the response of life support systems to environmental changes is a formidable challenge, which is addressed in several of the papers of this issue. The core of this issue amounts to understanding how environmental changes at the global scale lead to changes on individuals, but also impose selective pressures upon populations, and may lead to changes in diversity, at the genetic, phenotypic, and at the species levels. In essence, the problem is to bridge across very different spatial scales, from one cubic metre of ocean or one square metre of land, to the global scale, a change in linear distance of a factor 10^7 . To paraphrase Levin (1992), 'the description of pattern is the description of variation, and the quantification of variation requires the determination of scales'. A related issue is that organisms that interact with the environment do not probe the same physical space, although they are geographically located at the same position. This is because living creatures differ in their life-history stages and traits, but also more simply because they vary enormously in size, from 10^{-6} m in oceanic picoplankton to ca. 100 m for a whale and the largest living trees, a change in body size of a factor 10^8 in eukaryotes only. These creatures also experience widely varying spatial and temporal scale through dispersal and dormancy.

This review of the problem of pattern and scale in ecology is organised around four foci, each of which represents research areas where this problem has been of paramount importance in recent years, and which are likely to drive much research in the years to come. First, I will review new approaches to reconcile the ecological and evolutionary temporal scales. Then, I will turn to a research field that has long been disconnected from evolutionary and population biology: ecosystem science. The study of global change biology is poised to bridge this gap, and research in this area places a strong emphasis on scale and pattern. Third, I will explore the frontiers of the organism, with an emerging synthesis between systems

biology and ecology, largely driven by the analysis of network patterns. Finally, I will revisit the classic theme of spatial patterns in ecology.

COUPLING ECOLOGICAL AND EVOLUTIONARY SCALES

Complex systems differ in one fundamental way from other systems, in that their organisation is changed by the environment they themselves create through evolutionary processes. Traditionally, in ecology the study of ecosystem processes has been disconnected from that of evolutionary processes, under the argument that ecological processes acted over much smaller timescales than evolutionary ones. Over the past two decades, much progress has been made towards an understanding of the coupling between ecological and evolutionary temporal scales, as is briefly reviewed here.

Pace of evolution

How much does evolution impact population dynamics? This is not only the first natural question to ask in the study of complex adaptive ecological systems but it is also of fundamental applied relevance in studying the influence of climatic changes on biological diversity (Parmesan 2006; Savolainen *et al.* 2007). Evidence for an explicit coupling of temporal scales between ecology and evolution has accumulated relatively recently, although theoretical work had been conducted in the 1990s (van der Laan & Hogweg 1995; Abrams & Matsuda 1997). In experiments of rotifers preying on algae, Yoshida *et al.* (2003) compared single-clone algal cultures to multi-clone cultures. They found that the period of oscillations and the phase between predator and prey were dramatically affected by whether the prey could evolve (Fig. 1). In the multi-clone experiments, therefore with the possibility of prey to evolve, low-food value prey clones persisted in the over-grazed system and high-food value prey clones achieved competitive dominance after the predator population had crashed. This study shows that evolution may alter the trajectory of an ecological process if the heritable phenotypic change occurs sufficiently quickly.

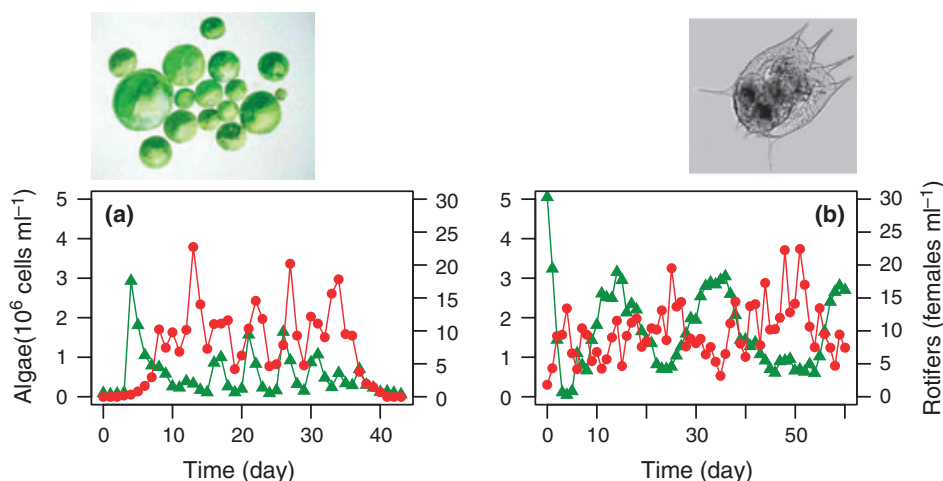


Figure 1 Experimental cycles of the prey algae *Chlorella vulgaris* (green triangles) and the predator rotifer *Brachionus calyciflorus* (red circles) populations in a chemostat system. In panel (a), the initial algal population was descended from a single algal cell, and the opportunity for advantageous algal genotypes to arise by mutation was minimised. This system exhibited classical predator–prey cycles with increases in prey abundance followed by increases in predator abundance after a quarter-period lag. In panel (b), the initial algal population was drawn from multiple sources and genetically variable. The cycles were longer and the oscillations in predator and prey abundance were almost exactly out of phase. Redrawn from panels b & g in Yoshida *et al.* (2003).

A wonderful example of how evolutionary dynamics is coupled with ecological dynamics in the wild is given by the Darwin's finch *Geospiza fortis*. Grant & Grant (2006) reported spectacular changes in beak size over a 40-year period (for a detailed review, see Grant & Grant 2008). In Darwin's finches, beak size is essential to forage on the seeds which they feed upon, and it is a heritable trait (Boag 1983). Further, beak size conditions the ability of the bird to crack seeds open, the major food income of *G. fortis* (Herrel *et al.* 2005). In 1977, a drought led to a decline of small-beaked *G. fortis*, because of a shortage of small seeds. The situation returned to the pre-1977 situation in 1983 after an intense rainy season. In 2004, the immigration of a competitor, *Geospiza magnirostris*, resulted again in a character displacement of the *G. fortis* population towards smaller beak sizes. Even more remarkable – and important for the point here – is the fact that the developmental basis for rapid changes in the shape of Darwin's finch beaks has been unravelled (Mallarino *et al.* 2011), offering a mechanistic basis for trait change observed in the wild.

The interplay between ecological and evolutionary dynamics can be modelled by focussing on a single species using an extension of Fisher's covariance equation (Frank & Slatkin 1992). Its instantaneous population growth rate r changes either because of changes in a heritable trait z (think of beak size in Darwin's finch), or because of a change in its ecological environment k (think of seed abundance). Hence, Hairston *et al.* (2005) suggested that the partial derivative of $r(z, k)$ against z , denoted $\partial r(z, k)/\partial z$, reflects the changes in the population growth rate due to trait change (and not due to changes in abundance). According to the chain rule

$$\frac{dr}{dt} = \frac{\partial r}{\partial z} \Big|_k \times \frac{dz}{dt} + \frac{\partial r}{\partial k} \Big|_z \times \frac{dk}{dt}$$

The right hand side of the equation has two terms: the first includes the effects of evolutionary dynamics and the second that of ecological dynamics. Hairston *et al.* (2005) went on to partition out the two effects. They were able to show that in *G. fortis*, evolutionary change in body and beak size of *G. fortis* was twice as fast as the ecological dynamics over the period 1976–1990. Of course, not all trait variation can be ascribed to evolution, for non-heritable trait variation is a conspicuous feature in populations (Gienapp *et al.* 2008), but this framework provides was successful at relating models and data. Since a central goal in ecology is to develop models that provide an integrative framework to understand how and when processes act at the same scale, the attempt to synthesise timescales, and see how the players contribute to changing their theatre, is a result of foremost importance in ecology (Schoener 2011).

Ecosystem consequences of evolution

The above research aims at unravelling the consequences of environmental processes on species evolution. A parallel question is: what is the influence of species-level evolution on the dynamics of ecosystems? Several theoretical approaches to this question have recently been reviewed by Fussmann *et al.* (2007), pointing to the profound role that evolution may have on ecosystem functioning. Recent experimental research has been conducted using a fish species as models: the guppy (*Poecilia reticulata*). Long-term research on guppies of Trinidad freshwaters has demonstrated the potential for evolution on reproductive and foraging traits, traits that were shown heritable (Reznick *et al.* 1997). Specifically, populations that have been exposed for a long period to a predator (a cichlid fish *Crenichilia alta*), attain

maturity at an earlier age and smaller size, produce more and smaller offspring per litter and devote more resources to each litter. Food availability for guppies varies with environmental factors such as forest canopy cover, such that less canopy cover favours the development of a larger algal crop, the primary food of guppies. Palkovacs *et al.* (2009) developed an experimental set-up in mesocosms, where they quantified how guppies that had been adapted to either high predation or low predation level differed in their impact on ecosystem structure and function. Guppy phenotypes were shown to have an impact on ecosystem processes independent of density: mesocosms with the high-predation phenotype had higher algal standing stocks but lower biomass-specific gross primary productivity, and a lower total invertebrate biomass (Palkovacs *et al.* 2009). A similar study with the threespine stickleback yielded comparable results (Harmon *et al.* 2009). The guppy and stickleback studies, together with recent theoretical work (Fussmann *et al.* 2007) represent a formidable effort to test the effects of evolution on ecosystem functioning, and they confirm that if the environment has a potential influence on species evolution, the reverse is also true.

However, eco-evolutionary dynamics models are still restricted in their scope. In the aforementioned examples, the environment is modelled through the dynamics of another species, the plant resource in the case of Darwin's finches and the copepod predator in the case of the guppy. A general predator–prey model is thus sufficient to reproduce their dynamics (Abrams & Matsuda 1997). A perspective for this research is to explore how this dynamics scales up from two species to the community level, which involves understanding how evolution shapes interacting networks (Melían *et al.* 2011), a theme that I will return to below. Another question is whether such patterns of eco-evolutionary dynamics will persist across spatial scales. In normal situations, adaptive divergence should decline with weak selection and increasing gene flow, but counter-intuitive results are expected in the presence of eco-evolutionary dynamics of several interacting species in networks.

THE SCALES OF GLOBAL CHANGE

A second illustration of the problem of pattern and scale in ecology that was in its infancy two decades ago is offered by global change biology. At that time, ecosystem science and evolutionary biology were perceived as disconnected, and Levin (1992) pointed out that this disconnection was a great challenge. It would be an overstatement to say that today this challenge has been overcome, but major studies have emphasised the role of adaptation in mitigating global climatic change (Hetherington & Woodward 2003), and have interpreted current biogeochemical functions in the light of the Earth's geological history (Wortmann & Paytan 2004; Falkowski *et al.* 2008). Here, I briefly review how ecosystem science has attempted to solve its internal problems of scale.

Scaling primary production from cells to the globe

A natural currency to measure these couplings is the carbon unit. Net primary productivity (NPP) is the amount of carbon fixed in the biosphere by unit area and time (Field *et al.* 1998). What are the regional contributions to global primary productivity worldwide, and how should global change alter them? This is a difficult question because we know that the carbon cycle is highly variable at all temporal scales (Falkowski *et al.* 2000; Fig. 2). One of the great suc-

cesses in ecosystem science since 1992 has been to wed empirical data and models, and to move towards predictive models of the biosphere. Much effort is still ahead, but this should not overshadow these achievements.

In terrestrial ecosystems, estimating the global NPP has relied on combining a number of independent techniques, some based on top-down scaling, others based on bottom-up scaling. In the former category, remote sensing products have been critical to describe vegetation types and their phenology (Running *et al.* 2004). Detailed measurements of the chemical composition of the atmosphere, combined with ingenious inversion techniques using global circulation models have also helped constrain regionally the carbon cycle (Tans *et al.* 1990; Gurney *et al.* 2002). Eddy-flux correlation techniques to measure exchanges of carbon dioxide between ecosystems and the atmosphere have also seen an exponential growth over the past two decades (Malhi *et al.* 1999; Baldocchi 2003; Luyssaert *et al.* 2007). As the CO₂ molecules are drafted above vegetation canopies by wind, which form eddies at the contact with the ground boundary, the temporal pattern of carbon fluxes at the atmosphere-vegetation interface shows a power-law pattern typical of turbulent flows (Baldocchi 2003). Such eddy-flux covariance techniques have provided a tremendous wealth of information across ecosystem types. Of course, these data must be assimilated to get at estimates of NPP values, and this is best done using vegetation models. Of special relevance to the point made here is Moorcroft *et al.* (2001)'s Ecosystem Demography (ED) model, which implements a method to up scale the individual-based processes of a forest model to the region. Specifically, ED approximates a microscopic model by a macroscopic one (Durrett & Levin 1994) through a method for scaling from the forest dynamics to a region through a system of differential equations. This approximation ignores the individual details and focusses on the ensemble averages (Bolker & Pacala 1997). If a suitable set of boundary conditions is provided, together with a distribution of waiting times since the last disturbance of forest patches, this method offers a rapid means for determining the regional dynamics of the vegetation at a coarse scale. This approach is currently one of the most promising ones for assimilating data across scales, especially including high-frequency environmental variables (Medvigy *et al.* 2010).

The study of the oceanic carbon cycle has followed a parallel path. The development of optical imagery (McClain 2009) and scaling

models (Antoine & Morel 1996; Behrenfeld & Falkowski 1997) has made it possible to infer NPP from chlorophyll concentration, resulting in remarkably accurate oceanic NPP maps (Gregg *et al.* 2005). Even more surprising is the finding that tiny creatures such as the picoplankton (less than 2 µm), contribute a significant fraction of global oceanic NPP (Uitz *et al.* 2010). Picoplankton differs from diatoms and other classically studied microplanktonic groups (> 5.0 µm), and still represents a poorly known reservoir of biodiversity (Vaulot *et al.* 2008). Bottom-up scaling methods through mechanistic have also been applied to the oceans. Various classes of primary producers of plankton have now been integrated in dynamic green ocean models (Le Quéré *et al.* 2005). One remarkable example of such a modelling effort is the attempt by Follows *et al.* (2007) to simultaneously simulate the oceanic biogeochemical cycles and the biogeographical organisation of biological diversity. Because of the complex nature of the couplings between the oceans and the atmosphere, scenarios for the future remain hypothetical. For instance, there remains considerable uncertainty on future changes in oceanic NPP (Henson *et al.* 2010), and more generally for global change scenarios (Moss *et al.* 2010).

Scaling metabolism from cells to the globe

One of the most classical illustrations of the importance of scale in biology is allometry, the relation of body size to anatomical, physiological, behavioural and ecological features (Calder 1984; Niklas 1994). Animal metabolic rate appears to show a $\frac{3}{4}$ power-law relationship with body mass (Kleiber 1947). Extraordinary efforts have been paid to test the generality of this pattern empirically (see e.g. Mori *et al.* 2010 in plants). West *et al.* (1997) attempted to derive the $\frac{3}{4}$ power-law scaling from first principles, assuming that respiratory and vascular systems are tree-like networks (e.g. from aorta to capillaries) and that exchanges at the capillary scale is limiting metabolic rate. This result has spurred considerable controversy because of its simplicity but also because the underlying assumptions can be readily tested by physiologists (Biro & Stamps 2010). Several excellent recent articles have reviewed the mathematical derivation of this model, and the nature of the assumptions underpinning it (Savage *et al.* 2008), and I will not further delve into this topic. The point I want to make here is simpler: the underlying idea of allometry to factor out the role of body size should help bridge across physiology and ecosystem science. This idea has been pursued by Enquist *et al.* (2003), Allen *et al.* (2005) and López-Urrutia *et al.* (2006), but in these studies the problem of body-size scaling has turned out to be far less relevant than that of the relationship between ecosystem-level metabolic rate and temperature.

At the ecosystem scale in terrestrial systems, metabolic rate is the compound of plant respiration (both above and below-ground parts), plus heterotrophic respiration of soil decomposers (Malhi *et al.* 1999). Across ecosystems, heterotrophic respiration varies from 25% to 50% of total respiration (Luyssaert *et al.* 2007). Recently, Vargas *et al.* (2010) have conducted a high-frequency monitoring of soil respiration in three ecosystems. Using wavelet transform analyses, they have explored the scale at which environmental variables (soil moisture and temperature) should correlate with soil respiration (Fig. 3). Their analysis shows that although soil respiration is expected to increase with moisture and with temperature, it is not easy to predict daily changes in soil respiration. Thus, at fine temporal scales, the dynamics of soil respiration is far from simple to model. However, under the assumption that

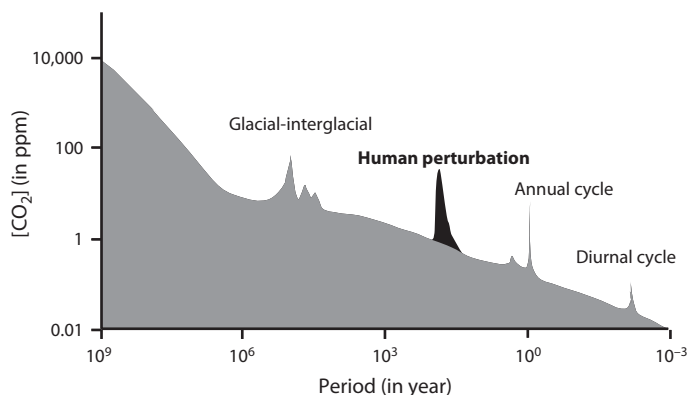


Figure 2 Schematic variance spectrum for the concentration of atmospheric CO₂ over the course of Earth's history. The impact of human perturbations on the decade-to-century scale is depicted in black, and show a unique signal. Redrawn from Falkowski *et al.* (2000).

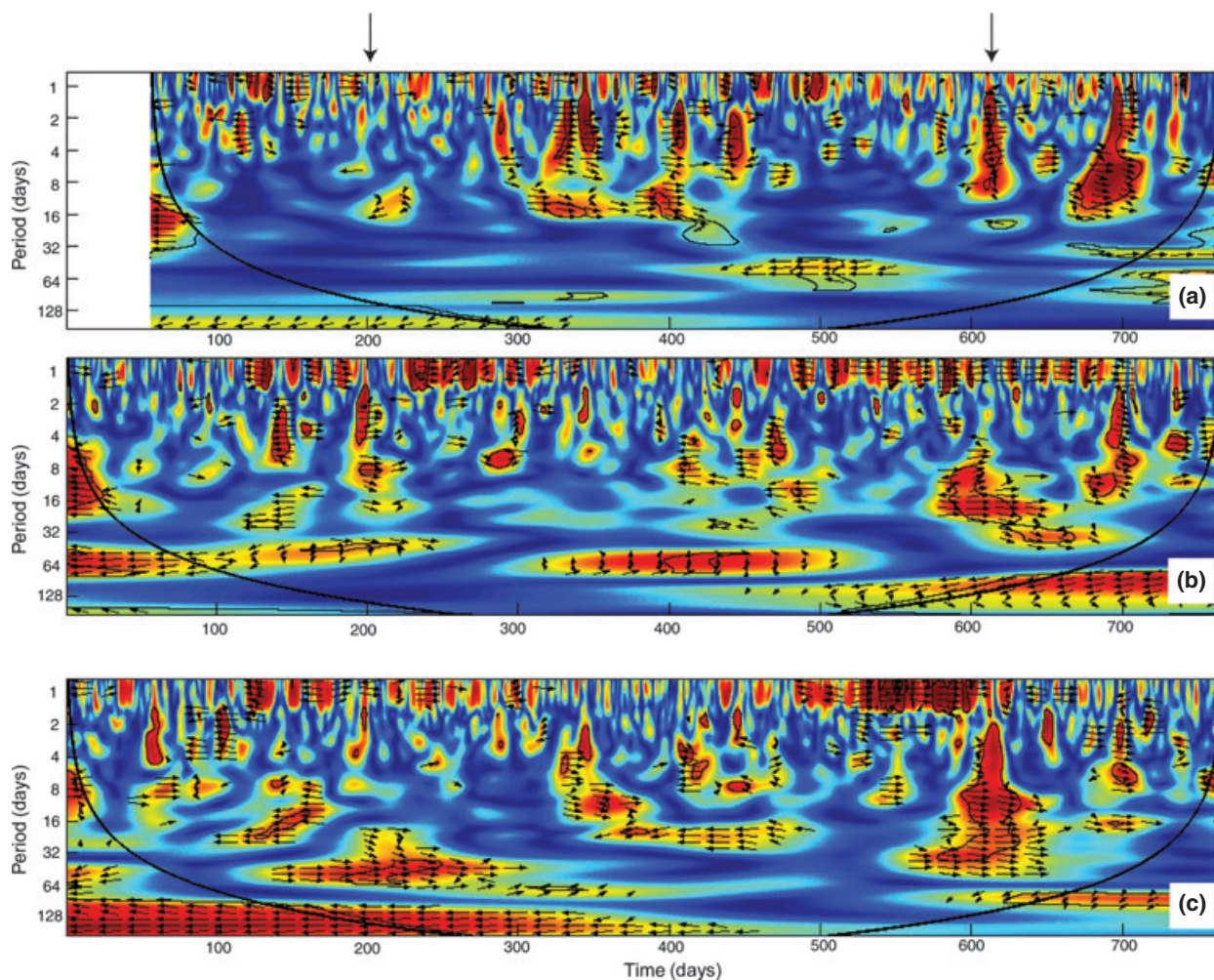


Figure 3 An example of wavelet analysis for an ecological problem. Correlation between soil CO₂ production and soil water content in three vegetation types: (a) mature woody vegetation, (b) young woody vegetation and (c) herbaceous meadow, during 2 years. Colour codes for power values between the two variables: from dark blue (low) to dark red (high). Black contour lines represent the 5% significance level. The phase difference is shown by arrows: in-phase pointing right (no lags between time series), off-phase pointing in other direction (lags between time series). Thick black line indicates delimits the region not influenced by edge effects. Arrows at the top of the panels indicate the approximate date of summer rainfall events. From Vargas *et al.* (2010).

all the cells of an ecosystem have similar temperature dependence of metabolic rate, one should be able to obtain a ‘macroscopic’ relationship.

At the cellular level, biochemical reaction rates are expected to vary with temperature proportionally to a factor, $\exp(-E/kT)$ where E is the activation energy of the reaction, T is the temperature (measured in Kelvin) and k is Boltzmann’s constant ($k = 8.617 \times 10^{-5}$ eV/K), as first derived by Arrhenius in the 19th century (Lloyd & Taylor 1994). At the ecosystem scale, Lloyd & Taylor (1994) showed that the dependence on temperature of soil respiration rate, R_T , is modelled by the following equation: $R_T = R_{10} \exp[E(1/kT_{10} - 1/kT)]$. Conventionally, R_{10} is the ecosystem respiration rate at $T_{10} = 283.15$ K (or 10 °C). Plotting empirical data, they found that $E = 0.55$ eV yielded a relatively good fit. The same relationship was proposed at the organism scale by Gillooly *et al.* (2001), who found activation energies ranging between 0.41 and 0.74 eV across organism groups, close to Lloyd & Taylor’s estimate (see also Yvon-Durocher *et al.* 2012s recent analysis). This suggests that temperature change has a similar effect on all the living creatures in an ecosystem, that is, it is invariant with scale.

For much of its history, ecosystem science has been concerned only with the fluxes of matter and energy at a local scale (Golley 1993). The problems of scaling from organism to ecosystem, and from ecosystem to the globe are fortunately now better integrated into this discipline.

MODULARITY IN INTERACTION NETWORKS

Levin’s (1992) study was also influential at bringing complex systems to the forefront of the ecological research agenda. Biological systems are inherently hierarchically structured and modular (Simon 1962; Hartwell *et al.* 1999). Modularity allows redundancy because the flow of information is quickly and evenly distributed within the module, and also resilience since any disruption of the system is buffered by this redundancy (for a mathematical definition of modularity, see Appendix S1). This has major consequences for the cellular and developmental machinery of organisms (Wagner *et al.* 2007), but also for the stability of ecological systems (Ives & Carpenter 2007). This concept was poised to become central to ecological thinking back in 1992 (Sugihara *et al.* 1989), and it has

indeed risen to dominance, for it offers ways to relate local interactions among individuals and emergent patterns at the community level. There are two different issues to be discussed here. The first is that individuals are generally not assorted randomly, and the scaling up of interactions from the individual scale to the community scale depends on the details of the fine-scale assortment. The second issue is that, while addressing the issue of modularity across scale in ecological systems, we should seek common features, and possible conflicts, in the emergence of modularity among individuals and within individuals.

Individual variation and interaction networks

Ecologists have traditionally studied the patterns created by the tangled web of ecological interactions among species (Paine 1980). The analysis of species-level interaction networks shows that they are typically modular (Sugihara *et al.* 1989; Melián & Bascompte 2004), and this has important implications for scenarios of biotic extinctions (Dunne *et al.* 2002). However, food web theory based on species graphs bears little empirical significance (Paine 1980; Polis 1991): ecological interaction networks should be quantified based on what individuals do, rather than just who eats whom among species. Intraspecific variation leads to a modulation of the strength of interactions through time (Tylianakis *et al.* 2007; Ings *et al.* 2009), and to a dynamic and individual-based view of ecological networks (Ings *et al.* 2009; McCann & Rooney 2009; Melián *et al.* 2011).

Individual-based interaction networks build on a long-standing tradition in population ecology. Each individual differs from its neighbours, in part because its genetic makeup is unique, in part because its history is unique. Population biology and life-history theory both strive to make sense of individual variation, and explore whether regularities exist across individuals and what causes them (for a recent review, see Bolnick *et al.* 2011). Even more importantly, each individual typically interacts with a small number of its conspecifics during its lifetime, and these opportunities are the means by which experience is acquired. In humans, the study of networks of social interactions has become a large part of modern sociology. The fact that individuals in conspecific assemblages are modularly related is of great importance for the parasites that thrive on us, because they may find it easier to spread within than across modules. For instance, the rate of spread of an epidemic depends on the precise structure of this individual interaction network (Keeling & Rohani 2008; Salathé & Jones 2010).

The problem of how to empirically measure individual-based networks is a serious one. In food webs, both stable isotopic signatures (Vanderklift & Ponsard 2003) and environmental DNA techniques may be used (Taberlet *et al.* 2012). In more generalised networks, interactions can be measured directly via the real-time monitoring of individual movement (Salathé & Jones 2010; Katz *et al.* 2011), or the measurement of chemical cues, such as signalling across plants (Unsworth *et al.* 2009) or quorum sensing in bacteria (Diggle *et al.* 2007).

Conflicts among scales

In some cases of great relevance to ecology and evolution, individual interactions can lead to the emergence of altogether new behaviour at the macroscopic scale. In slime moulds, the multicellular habit is directly related to the formation of fruiting bodies (Bonner 1993). One major advantage of cell differentiation in multicellular organisms

is a division of labour to facilitate dispersal. Velicer & Yu (2003) studied how the bacterium *Myxococcus xanthus*, has evolved the ability to display a multicellular stage, able to glide across soft surfaces (Berelman & Kirby 2009). They studied some strains of *M. xanthus* that exhibited socially dependent swarming through enhanced production of an extracellular fibril matrix that binds cells together. Though costly to individuals, fibril production greatly enhances population expansion in groups of interconnected cells (Velicer & Yu 2003). The resulting multicellular structure behaves as an efficient predator of other microbial species relying on chemotaxy to cue its prey. Berelman & Kirby (2009) call such swarms a 'bacterial wolfpack', and show impressive photographs of the predatory behaviour of these swarms. A similar type of collective behaviour, biofilm development, has been invoked to explain the increased virulence of the bacterium *Pseudomonas aeruginosa* in acute forms of infections (Diggle *et al.* 2007).

In the above, the collective behaviour is beneficial to the species but comes at a cost for the individual. However, another conflict in levels of selection occurs when the emergence of a novel strategy at the individual-scale results in a detrimental outcome at the macroscopic scale. A well-known example of such a selfish strategy is observed with the development of neoplastic cells within a cancer tumour (Leroi *et al.* 2003; Merlo *et al.* 2006). This is a version of the commons problem, whereby 'common-pool' resources tend to be over-depleted by a few free-riders, at a cost for the society (Ostrom *et al.* 1999). This concept has been central in rethinking the management and institutional governance of environmental crises (Ostrom *et al.* 1999; Ostrom 2005). In ecology, understanding how conflicts operate among scales of organisation is essential to appraise the emergence of complexity and the modularity in individual-based interaction networks. As this principle is a general one, it should also apply below the organismic level, an aspect to which I now turn.

Systems biology and reverse ecology

One view of the emergence of complexity in biology involves autocatalytic chemical reactions with molecules that are both substrates and catalysts (Maynard-Smith & Szathmáry 1995). The resulting compartmentalisation of forms and functions appears to be one of the most universal features of life, hinting to the fact that common features of symmetry breaking lead to increasing complexity of life (Anderson 1972). Seeking for analogies between modularity in the networks of cellular biology and that of ecology goes some way towards exploring the commonalities of pattern formation across scales. One illustration is Jeong *et al.* (2000)'s analysis of metabolic networks showing that these display scale-free features: most of the enzymes within the network have only few connections, while a few enzymes, so-called hubs, are highly connected. There is more than a point of analogy to make between metabolic networks and ecological interaction networks: modular cell biology, *sensu* Hartwell *et al.* (1999), has now moved to the frontiers of ecology, and deserves special scrutiny here.

What if we could combine ecological networks and metabolic networks? Ecological interactions among species are often (though not always) mediated through chemical signalling. Exciting developments have recently been achieved that shed a new light on this question. Stolyar *et al.* (2007) studied the influence of a mutualism between a sulphate-reducing bacteria and a methanogen, which controls the production of methane in many environments, such as the digestive tract of ruminants. They were able to model this system as a single

metabolic network of the two mutualistic species. Their model accurately predicted several ecologically relevant characteristics, such as the flux of metabolites and the ratio of cells in the two species during growth. Hence, reconstructed metabolic networks and stoichiometric models can serve not only to predict metabolic fluxes and growth phenotypes of single organisms but also to capture key ecological features in the interaction of simple bacterial communities. In effect, this suggests that when the full metabolic network of a species is known, its ecology is defined by the interactions of this network with the environment, thus enabling us to infer from the structure of biological system information about the environment in which it evolved, a method called ‘reverse ecology’ (Parter *et al.* 2007).

Parter *et al.* (2007) computed the modularity of a large number of bacterial species with known metabolic networks and justified that the fraction of transcription factors out of the number of genes could be used as a measure of environmental variability. They could show that metabolic networks of organisms in variable environments were significantly more modular than networks of organisms that evolved under more constant conditions (Fig. 4). This suggests that modularity may be used as a measure of ecological niche breadth. Borenstein *et al.* (2008) further suggested that when the full metabolic network of a species is known, its ecology is defined by the interactions of this network with the environment. Exploring formally which nodes of the network represents exogenously acquired compounds results in defining an ensemble of ‘seed compounds’ (Fig. 5). This concept was useful to distinguish which key metabolic features were lost in parasitic organisms compared with free-living ones, and in confirming that the metabolic machinery of parasites is simpler than that of free-living organisms. Finally, Peregri n-Alvarez *et al.* (2009) conducted a comparative study of the structure of metabolic networks, and they have pointed to a limited number of modules representing core activities, and conserved across the tree of life, while more peripheral activities tended to be

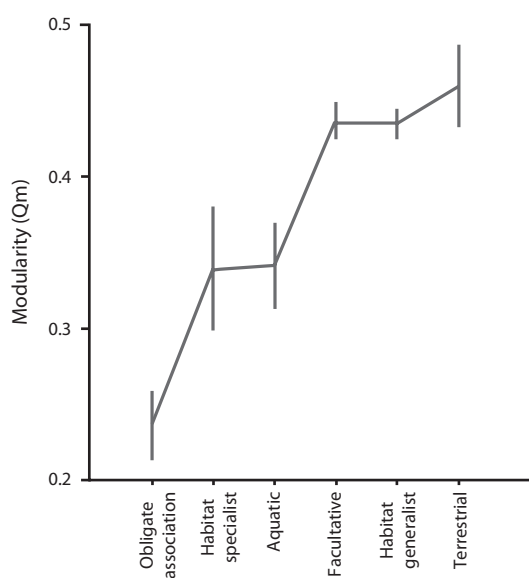


Figure 4 Normalised modularity measure Q of bacterial metabolic networks vs. the ecology of the organism. Organisms were grouped into classes ranging from the most specialised to the least specialised. Terrestrial (soil) organisms appeared to have the most variable ecology. Mean and standard error of Q are presented for each class, and the Q index was normalised to account for differences in network size across species. Redrawn from Parter *et al.* (2007).

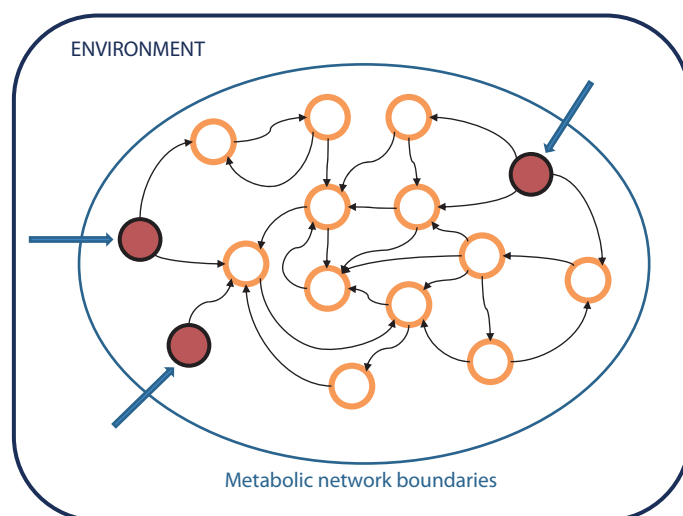


Figure 5 Reverse ecology of a metabolic network. A schematic representation of the interaction of a metabolic network with its environment. Compounds highlighted in red must be externally acquired from the environment. In the metabolic network of the bacteria *Buchnera*, the set of externally acquired compounds is of 61 chemicals of 314 compounds. Redrawn from Borenstein *et al.* (2008).

more labile across species. Core metabolic activities should be highly resilient to failure, and this is achieved through a tight integration. Together these studies suggest that the ‘reverse ecology’ approach does not only help rethink classical questions in ecology, it is also an umbrella for a novel integration between ecology and cell biology (Oberhardt *et al.* 2009; Gudelj *et al.* 2010).

Exploring network patterns across levels of organisation offers an important lesson. The traditional scales of ecology are spatial and temporal, but the problem of scale could be also addressed in the abstracted multidimensional space of an interaction network. A goal of this section was to emphasise that reasoning about scales in ecology leads naturally to question how modularity arises evolutionarily and what its ecological consequences are. This viewpoint blurs the traditional view of the individual, and some central ecological questions need to account for processes both within and among individuals.

SPATIAL PATTERNS OF DIVERSITY

The fourth and final theme is that of spatial patterning in biological diversity. Looking at the spatial map of a tree species, the ecologist asks why individuals are locally clustered and whether this clustering changes across scales (Fig. 6). This is a general feature of spatial species maps: individuals are patchily placed in space, and this patchiness varies with the grain of observation (Hutchinson 1953). A striking example is offered by glittering sea creatures. The unicellular oceanic plankton *Emiliana huxleyi* forms massive blooms detectable using optical imagery (McClain 2009). If oceanic movement is crucial in determining the spatial arrangement of *E. huxleyi* populations over regions, other processes such as limited dispersal explain the small-scale dynamics of these blooms (Tyrrell & Merico 2004). Indeed, dispersal limits the opportunities for species spread even in the absence of environmental barriers. This feature is best illustrated using toy models of pattern formation (Box 1). One generic feature emerging from toy models is that local dispersal is essential to explain pattern formation.

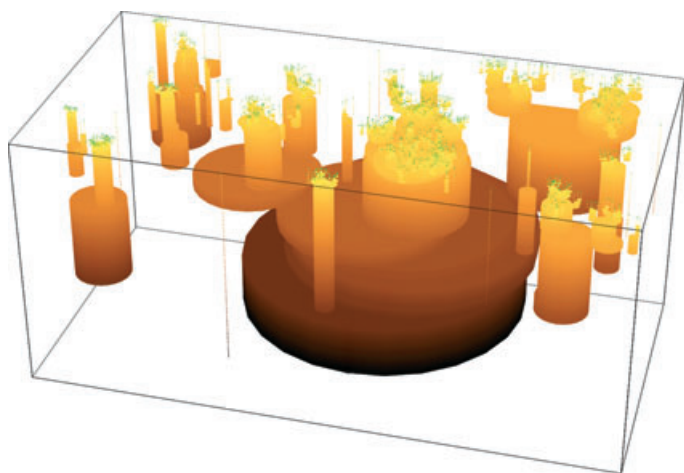


Figure 6 Spatial distribution of 1404 trees of *Mallotus penangensis*, Euphorbiaceae in the 50-ha plot of Pasoh, Malaysia. The Figure shows a three-dimensional graph of clusters. The X - and Y -axes correspond to the length and width of the 50-ha plot. The Z -axis corresponds to the value of the clustering parameter. The colour also corresponds to the value of this parameter (from green to black). As the clustering parameter increases down the Z -axis, larger clusters form. Each cluster is represented in the Figure by a circle centred at the centre of mass of the cluster. The radius of the circle equals the mean distance of the trees in the cluster to its centre of mass. From Plotkin *et al.* (2002).

Ecologists have long been faced with the issue of scale mismatch in the study of the dispersal process. In the late 19th century, the British botanist Reid calculated that the recolonisation rate of England by oaks after the last glacial period implied a colonisation speed of c.a. 100 m/year (Clark *et al.* 1998). This was far more than what ecologists had measured in the field. It is fortunate that theory and empirical patterns may be reconciled. In a seminal mathematical analysis, Kot *et al.* (1996) showed that the regional population dynamics not only depends on the propensity of individuals to disperse but also on the whole shape of the dispersal kernel (the probability $P(r)$ that a propagule disperses r metres away from its parent, in any direction). The population front displaces at a speed proportional to $v = \int_0^\infty rP(r) \times 2\pi r dr$, the first moment of the distribution. If the dispersal kernel declines slowly with distance, for example, a shape $P(r) = A/(1+r^\alpha)$, and if $2 \leq \alpha < 3$, it may be shown that the population spreads at an unbounded speed (Kot *et al.* 1996). In this situation, traditional models of spatial dispersal fall apart: the speed of spread increases with time. Such anomalous diffusion behaviours have been studied both in plants and animals (Nathan 2006; Edwards *et al.* 2007), and they are of direct relevance in the study of how species respond to global change and thus to determine the threshold for population and metapopulation extinctions. Long-distance dispersal is also crucial to explain larger scale biogeographical patterns such as beta-diversity (Chave & Leigh 2002) and island biogeography (Emerson & Gillespie 2008).

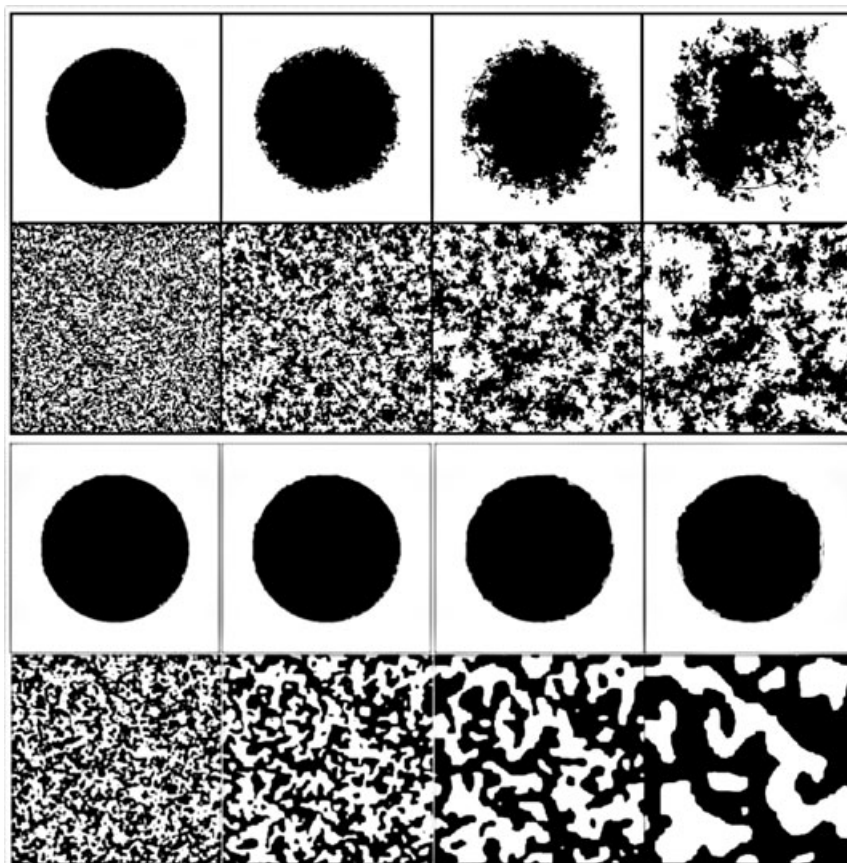


Figure 7 Dynamic patterning in two toy models: the voter model (top two rows) and the Ising model at zero temperature (bottom two rows) on a 256×256 lattice with toroidal boundary conditions. Snapshots at time 4, 16, 64 and 256 (left to right). Lines 1 & 3 show an initial bubble of radius 180, whereas lines 2 and 4 show random initial conditions with equal proportions. From Krapivsky *et al.* (2010).

Box1 Toy models of local dispersal

As dispersal is so closely related to pattern formation, it is useful to explore how this relation emerges in toy models. Fig. 7 illustrates two generic models of spatial patterning (the voter model and the zero-temperature Ising model, see Krapivsky *et al.* 2010) where the local rules combined with the information exchange between nearest neighbours generate a macroscopic pattern (see more details in the Appendix S1). Both models of Fig. 7 are assuming nearest-neighbour dispersal only. Now assume that, with some probability $m > 0$, vacated sites are occupied by offspring produced anywhere in the lattice. Even for very small m values, the spatial patterning depicted in the top part of Fig. 7 is destroyed, but the second model maintains its spatial structure (for small enough m). One learns two important messages with these toy models. First, although both models could be used to simulate the dynamics of two species in competition, apparently minor differences in the local dynamics of individuals result in radically different emergent behaviours. Second, the addition of long-distance dispersal strongly alters spatial patterning in some of the models. Hence, long-distance dispersal plays a key role on pattern formation in ecological community assembly.

Global diversity patterns

Patterns of regional species occurrence and abundance have long been the focus of biogeography. A general biogeographical pattern is the latitudinal diversity gradient, according to which the tropics have more species than temperate zones (Hillebrand 2004). Thanks to large-scale DNA-based screens of microbial diversity (Pace 1997), latitudinal diversity gradients have now been also quantified in microorganisms (Fuhrman *et al.* 2008).

In an important meta-analysis, Hillebrand (2004) performed an intriguing test. He included both studies where species richness was known from occurrences in grids and studies where species richness was known from local sites, possibly scattered unevenly across the globe. Although the latitudinal diversity gradient was observed in both cases, the decline of diversity with latitude was steeper and more marked in the former case. The latitudinal gradient of diversity is easier to detect if the local effects of biotic interaction, dispersal and stochasticity are averaged out in a coarse grained metric of diversity. Whether to treat biological diversity in a spatially explicit setting or not, and whether to consider the individual-scale or a grid-based description of diversity (Durrett & Levin 1994), has come to be one of the most important cornerstones of ecological enquiry. This distinction bears analogies with the distinction between the Eulerian (grid-based) vs. Lagrangian (particle-based) description of fluid movement in fluid mechanics (Flierl *et al.* 1999). One recent avatar of the debate of grid-based vs. individual-based description has manifested itself in species distribution models (Elith & Leathwick 2009).

Back to the latitudinal diversity gradient, attempts to provide a mechanistic understanding must combine ecological and evolutionary theory (Mittelbach *et al.* 2007). As the tropics tend to have a more stable climate, tropical organisms seldom are adapted to frost. Thus, tropical life is thought to be more suitable for a wide range

of species, and species lifetime longer the tropics are a 'museum of biodiversity'. Alternatively, the tropics may be more favourable to speciation than temperate zones, and act as a 'cradle' of biodiversity (perhaps because increased metabolism favours mutagenesis, Brown *et al.* 2004). Unfortunately, observing latitudinal diversity patterns alone sheds no light on which of the alternatives is the more likely. To disentangle this problem, as often in science, it is useful to look out of the box, and explore alternative patterns. By reconstructing phylogenetic trees in lineages that co-occur in tropical and temperate regions, it is possible to test whether the tropical species are more recent (suggesting higher tropical speciation rates) or more ancient. Weir & Schluter (2007) applied this line of reasoning to birds and mammals. They plotted the time since divergence of sister species pairs against the mid-point of occurrence of the species, and found that the splits in tropical species pairs tend to be older than in temperate zones, pointing to a higher speciation rate at high latitudes compared with the tropics. This counter-intuitive result may be due to the fact that tropical lineages have undergone explosive periods of diversification followed by a speciation slowing down (Rabosky & Lovette 2008). This analysis was criticised because the molecular clock applied to infer times of divergence may not be accurate (Nabholz *et al.* 2009), and that the systematics of tropical birds remains poorly known (Milá *et al.* 2012). Also, in addition to undergoing events of speciation and or extinction, lineages also radiate in space: a tropical species may have a sister species outside of the tropics (Wiens & Donoghue 2004). In a fascinating study of the marine bivalve fossil record, Jablonski *et al.* (2006) reported the time of first occurrence of bivalve lineages, and they showed that the vast majority of these lineages had originated in the tropics (in spite of the strong sampling bias towards temperate zones). They thus proposed an explanation for latitudinal diversity patterns where most of the lineages originate in the tropics, yet a fraction of these lineages subsequently expand polewards. This example illustrates that the latitudinal diversity gradient, indeed any spatial pattern, cannot be studied in splendid isolation.

Contingency in local species assemblages

Ecologists have long remained oblivious to large-scale process, and have ignored that the biodiversity problem is contingent on processes that act over much larger scales than the ones of classical ecological enquiry and should be readdressed by incorporating data from systematics, biogeography and palaeontology into analyses of community assembly (Ricklefs 1987). Hubbell (2001) proposed a quantitative framework to bridge these spatial scales. In Hubbell's model, individuals effectively compete for space in a local area. A species may go extinct locally, but the diversity is replenished through the continuous immigration of individuals from outside. Thus, the local and the regional scale are coupled through dispersal. Finally, species may go extinct at the regional scale, but the regional species pool is replenished through an implicit parameter that defines speciation. This simple model couples some of the crucial features of species diversity: stochastic local dynamics, coupling across scales and regional-scale dynamics. To facilitate the mathematical analysis of this model, Hubbell (2001) assumed that all individuals have the same prospects of reproduction and or death. This neutral premise has spurred considerable controversy: how could a theory of biodiversity be based on the ignorance of species differences? This is a case of exploring whether the details of the local

dynamics really matter to classical diversity patterns. Indeed, in spite of its simplicity, this model was successful at reproducing the species abundance distribution, or the species area curve (Hubbell 2001). Thus, arguably local details do not matter to understanding some patterns of diversity at the regional scale, at least patterns such as the species abundance distribution (for an explicit multi-scale framework generalising Hubbell's model, see Leibold *et al.* 2004).

Thus, if we are to quantify the imprint of biological processes on community assembly, beyond neutrality, we need to search for other community-wide patterns than simply the species abundance distribution. Measures of ecological distances based on ecological traits have been proposed to quantify community-wide character displacement (Dayan & Simberloff 2005; Kraft *et al.* 2008; Losos 2008). In addition, metrics related to the evolutionary distances of locally co-occurring species have featured prominently in this research area, in the wake of Webb (2000)'s seminal paper. Webb (2000) suggested that if competition really shapes community assembly, then co-occurring species should be phylogenetically more dissimilar locally than in the regional species pool. Conversely, they should be phylogenetically more similar locally than in the region if some lineages have specific adaptations for the habitat that the species assemblage occupies (think of succulence in desert-adapted plants). This idea has generated much exciting recent research (Emerson & Gillespie 2008; Cavender-Bares *et al.* 2009 for recent reviews).

Lawton (1999) famously wrote that it was time to move on from community ecology. His point was that local species assemblages are too complex and that intermediate scales have so much contingency that useful generalisations are hard to find. The decade following Lawton (1999) has shown that community ecology is actually a most fertile ground for ecological research, not only because it is the scale at which key conservation issues should be addressed (Simberloff 2004) but also because generalisations can be found across communities based on simple principles (Hubbell 2001; Brown *et al.* 2004). To their profit, ecologists have now abandoned the view that ecology should only be performed in small plots or Petri dishes but across sites interconnected through dispersal, and decoupled the details of the local community (Leibold *et al.* 2004), and Ricklefs (1987)'s plea for more integration with systematics, biogeography and palaeontology has now been realised.

OUTLOOK

Reflecting on the recent past of such crucial concepts as pattern and scale illustrates how fast our discipline has advanced and how well it has assimilated a cross-disciplinary view of the study of nature. It also points to new frontiers. The increased realisation that environmental problems impact our livelihoods across spatial and temporal scales has fostered much research in our discipline. An array of technological and conceptual developments has brought new inroads into these key problems. Such developments have increased awareness that it is essential to study ecological questions across scales, although limits to this statement should be pointed out. For instance, Wheatley & Johnson (2009) have recently reviewed the literature of wildlife research and reported that arbitrariness in the choice of study scale remains prevalent today even though these questions are of obvious relevance to conservation planning.

Here, I have selected four themes because they illustrate traditional questions in ecology where remarkable recent progress has

been achieved through a thorough rethinking of old questions: the reconciliation of the ecological and the evolutionary time scales; advances in ecosystem science and biogeoscience; the emergence of individual-based networks (and the increased focus on metabolic networks); and the integration of community ecology and biogeography, with a focal role of dispersal as the fundamental process that bridges across spatial scales. These themes are intertwined. For instance, I have purposefully left aside functional trait ecology, a topic that cuts across all four themes.

Although the problem of scale is arguably one of the most important in ecology, it should not be inferred that ecology is all about scale-free networks and power laws. As ecology was making definite and rapid progress, a line of research was in search of the grand unified theory for ecology. Science always benefits from sharing ideas across disciplines, but the notion that, unlike physics, ecology suffers from a lack of general laws (Lawton 1999) stems in part from a misperception of the successes of physics (Anderson 1972). Goldenfeld & Woese (2011) recently developed the view that physics has not been much luckier than biology in grappling with the study of complex systems, a study that biology was faced to at the outset. This suggests that in approaching novel frontiers of the study of complex ecological systems we need to pause about the challenge ahead of us, and avoid the development of language-culture to explain away the conceptual difficulties (Goldenfeld & Woese 2011). Once we enter the realm of complex systems, neither physics nor biology are well equipped to progress.

Levin's (1992) message was that a key to develop a predictive theory for ecology was in examining the patterns in nature and in developing theories that help assimilate observations across scales. I have argued that with the avalanche of data our discipline is accumulating, this lesson remains very true today and it should motivate us ecologists to combine empirical and theoretical research, but also embrace both the holist and the reductionist approaches, rather than specialise in either one of these.

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