

IDEA AND
PERSPECTIVEThe wealth of species: ecological communities,
complex systems and the legacy of Frank Preston

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Abstract

General statistical patterns in community ecology have attracted considerable recent debate. Difficulties in discriminating among mathematical models and the ecological mechanisms underlying them are likely related to a phenomenon first described by Frank Preston. He noted that the frequency distribution of abundances among species was uncannily similar to the Boltzmann distribution of kinetic energies among gas molecules and the Pareto distribution of incomes among wage earners. We provide additional examples to show that four different ‘distributions of wealth’ (species abundance distributions, species–area and species–time relations, and distance decay of compositional similarity) are not unique to ecology, but have analogues in other physical, geological, economic and cultural systems. Because these appear to be general statistical patterns characteristic of many complex dynamical systems they are likely not generated by uniquely ecological mechanistic processes.

Keywords

Community ecology, competitive sorting, complexity science, distance decay, ecological theory, neutral models, species–abundance distribution, species–area relationship, species–time relationship, statistical mechanics.

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Frank Preston (1950) published a little paper on ‘Gas Laws and Wealth Laws’ in *The Scientific Monthly*. In it he commented on the remarkable similarities between the Boltzmann frequency distribution of molecular kinetic energies in gasses, the Pareto frequency distribution of personal incomes in countries, and the frequency distribution of species abundances in ecological communities. After noting how such distributions might arise, he went on to remark – in comments which would now be politically incorrect in reference to personal incomes – about whether it is ‘wise to try to change the laws of nature’.

Interest in community ‘distributions of wealth’ (DOWs), in particular the species–abundance distribution (SAD), species–area relationship (SAR), species–time relationship (STR), and distance decay of compositional similarity (DD), have preoccupied community ecologists ever since Preston’s seminal papers (Preston 1948, 1962a,b, 1980; see also Williams 1964; MacArthur 1972; May 1975; Nee *et al.* 1991; Rosenzweig 1995; Nekola & White 1999; Gaston & Blackburn 2000; Hubbell 2001). As new, larger, and more comprehensive data sets have become available, the discipline of community ecology has been enlivened by

debate over which of several different conceptual frameworks or formal mathematical models might be necessary or sufficient to explain these patterns.

These debates have primarily had two foci. First, authors have argued about the relative roles of ‘competitive’ (deterministic ecological differences between species) vs. ‘neutral’ (stochastic processes of birth, death and dispersal) mechanisms in community assembly. This issue has been difficult to resolve as formal models invoking complete neutrality generate very similar outcomes to models that assume unique species-level abiotic requirements or strong biotic interactions (e.g. Bell 2000; Chave *et al.* 2002; Mouquet & Loreau 2003; Chave 2004; Tilman 2004; Gaston & Chown 2005).

The second focus has been about which particular mathematical distribution (and corresponding ecological mechanism) best describes empirical DOWs. This debate has been constrained by the fact that mathematical distributions having different mechanistic interpretations can be very difficult to empirically distinguish. For instance, it has proved extremely difficult to determine whether a particular SAD data set is best fit by a power law, truncated

log-normal, or zero sum multinomial (ZSM) distribution (e.g. McGill 2003a; Volkov *et al.* 2003; Chave 2004; Etienne & Olff 2005), and similarly whether a power law or exponential distribution best fits a given SAR/STR relationship (Loehle 1990; White *et al.* 2006). May (1975) and Connor & McCoy (1979) made these points decades ago for the SAD and SAR.

We regard as healthy the renewed interest in community ecology, and especially the focus on large-scale, multispecies macroecological pattern and process which are often not amenable to testing by manipulative experiments. But we also wonder whether the current framing of questions and tenor of debates are productive. Perhaps, as Preston suggested, DOWs are not the unique provenance of ecology, but rather are common properties of many seemingly disparate systems. If so, it may be best to seek explanations for these patterns that are as general as the systems that exhibit them.

To address this issue, we have extended Preston's examples to a broader selection of data sets spanning a wide range of physical and human economic, social and artistic systems. **Physical systems:** (i) Yearly precipitation averages for each of 1027 North American sites (see Nekola 2005). These data are based on 1-km resolution global precipitation maps created by the WORLDCLIM Project (<http://www.worldclim.org>); (ii) Mineral species richness from county to global scales, as reported by the MINDAT data base (<http://www.mindat.org>). Data represent the total number of minerals for the entire terrestrial globe, for 10 countries (Australia, Canada, Chile, China, India, Mexico, Namibia, Turkey, the UK and the USA), all the USA states (including the District of Columbia), all Canadian provinces/territories, and two selected counties per state. Areas for each unit were based on data provided with ArcMap 9.1 (ESRI, Redlands, California, USA). **Economic systems:** 2004 Stock volumes for all publicly traded corporations in the USA, based on data reported by Bloomberg (http://pages.stern.nyu.edu/~adamodar/New_Home_Page/data.html). **Social systems:** (i) Citation frequencies for all papers catalogued by the *Institute for Scientific Information* from 1981 to 1997 (<http://physics.bu.edu/~redner/projects/citation/isi.html>); (ii) the list of all commercially sold garden vegetable varieties in the USA and Canada from 1981 to 2004 as reported by the Garden Seed Inventory of the Seed Savers Exchange; (iii) the list of all ingredients reported in recipes for 10 global cuisines (Ethiopia, Hungary, India, Iran, Ireland, Korea, Mexico, Norway, Puerto Rico and Thailand) from Smith (1990). **Artistic systems:** (i) The number of unique words and total word length for the 1863 texts documented in Project Gutenberg as of 2000 (<http://www.mine-control.com/zack/gutenberg/>); (ii) concert setlists for 33 approximately evenly spaced Cowboy Junkies performances from 1987 to 2006 (<http://setlist.com>).

Using standard ecological protocols (e.g. 'octaves' or \log_2 bin widths for SADs and Jaccard's similarity in the calculation of compositional similarity between all pairwise combinations of observations for DD analyses), we treated each as if they were ecological data sets. All DOW analogues were calculated from the Cowboy Junkies example, as only this data set provided abundance data across multiple observations. For the remaining, analyses were limited to the DOW equivalents that could be assessed from the given data: SAD analogues for precipitation class frequencies, stock volumes and scientific citations; SAR analogues for mineral species richness and Project Gutenberg texts; STR analogues for North American garden seed offerings; and DD analogues for global cuisine and vegetable seed offerings.

These analyses corroborate Preston's observation that typical DOW patterns are by no means unique to ecological systems. North American precipitation classes, 2004 stock volumes, scientific citation frequency and song frequencies from Cowboy Junkies setlists (Fig. 1) are all similar to truncated log-normal or ZSM distributions with rare events being more frequent than abundant ones. Using code developed by McGill (2003a) the ZSM can be shown to well fit both the precipitation ($\theta = 55.173$, $m = 0.179$) and Cowboy Junkies setlist ($\theta = 89.446$, $m = 0.240$) data. Power law SAR and STR-like relationships are also widespread (Fig. 2), being observed not only for the accumulation of mineral species across space, but also for unique words as a function of book size and for unique vegetable varieties and Cowboy Junkies song performances as a function of time. The fitted relationships explained 46–99% of observed variance. Finally, nonlinear DD relationships are also common (Fig. 3), being evident in cuisine ingredient lists, the garden seed industry, and Cowboy Junkies setlists. For these examples, power law decay models fit best, accounting for 38–88% of observed variance.

The convergence between ecological and non-ecological community patterns is not limited to these examples. In his final *Ecology* paper, Preston (1981) documented rarity-enriched ZSM-like SAD analogues for the service life of restaurant drink tumblers, the static fatigue of glass and other materials, and first marriage age for Danish, UK and the USA women. Power law STR analogues have also been noted in comprehensive examination scores for degree candidates in the University of Oslo, Department of Biology and for Norsk Hydro stock prices on the Norwegian market (Ugland *et al.* 2005). And, given the convergence between the body-size distribution of beetles in Borneo tree canopies and cars in York and Heathrow Airport parking lots (Gaston *et al.* 1993), it appears such similarities may not be limited to DOWs.

These examples caution that the general mechanisms generating many familiar DOW patterns are not unique to ecology. Certainly, the processes of birth, death,

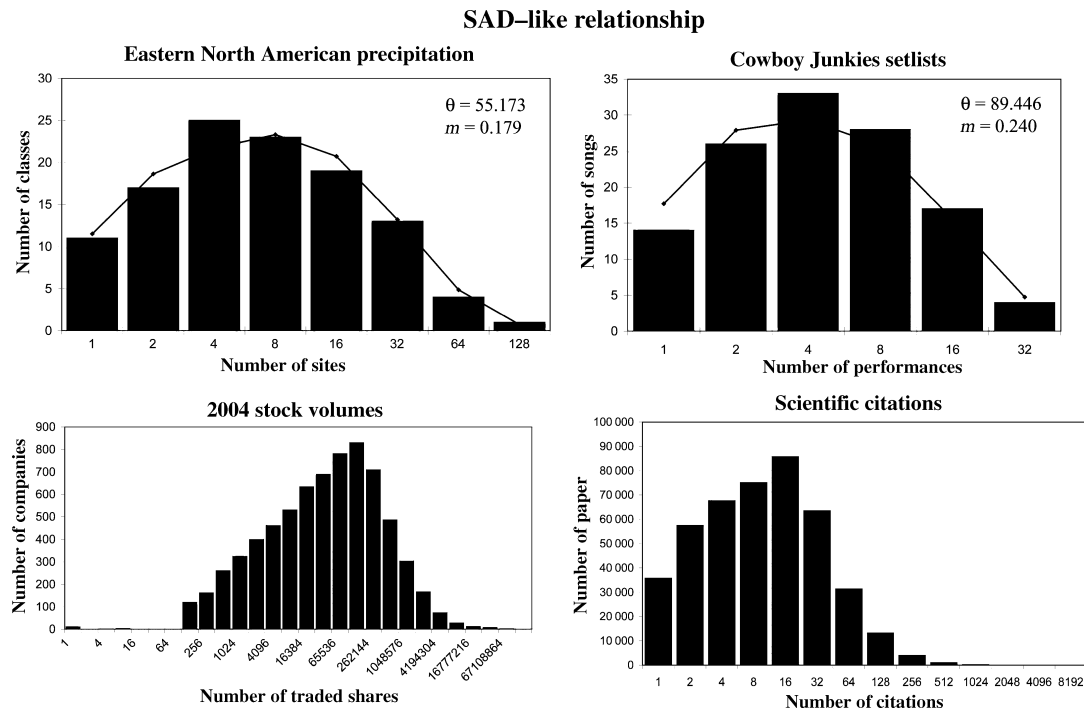


Figure 1 Species–abundance distribution analogues for non-ecological systems, including North American precipitation classes, stock volumes for all publicly traded US corporations, song performances for Cowboy Junkies setlists, and citation frequencies for scientific papers. All distributions have been binned into log₂ ‘octaves’. For precipitation classes and Cowboy Junkies performance frequencies, the best-fit zero sum multinomial distribution has also been calculated using code provided by McGill (2003a). These best-fit curves are presented as the graphed lines in both of these panels.

immigration and speciation invoked by Hubbell (2001), or the competitive tradeoffs invoked by Tilman (2004) or Chave *et al.* (2002) could not have generated the ZSM-like SADs for precipitation classes, paper citations, stock volumes, drink tumbler longevity, and marriage ages, or power law SARs/STRs for unique mineral, word, and garden seed occurrences, or comprehensive examination scores. Conversely, it seems unlikely that Cowboy Junkies performances mimic community ecology process, even though they display rarity-enriched SAD, power law STD and nonlinear DD patterns.

Preston (1950) concluded that the remarkable convergence between the Boltzmann, Pareto and SAD might be the result of ‘statistical mechanics’. Even though he could not identify the common underlying mechanisms, he urged scientists to ‘understand [this] law, and the causes that bring it about’. We question whether the recent revival of interest in ecological DOWs has advanced this goal. These congruent patterns seem to beg for some kind of explanation that is both more universal and also less explicitly mechanistic than the kinds typically sought and offered by community ecologists.

Over the last few decades investigations in the new interdisciplinary field of complexity science have begun to

address such issues. Complexity science developed as natural and social scientists sought to identify and explain common features exhibited by complex dynamical systems in such seemingly disparate fields as quantum physics, computer science, economics, sociology, political science, linguistics, astronomy, geology and meteorology. While a single definition for a ‘complex system’ remains elusive, a number of common features have been identified (Brown 1994a,b; West 2006a,b):

- (1) They are composed of many components of many different kinds.
- (2) These components interact with each other and the extrinsic environment in many different ways and on multiple spatial and temporal scales.
- (3) These interactions give rise to complex structures and complicated nonlinear dynamics.
- (4) These structures and dynamics are neither completely stochastic nor entirely deterministic, but instead represent a combination of randomness and order.
- (5) They contain both positive and negative feedback mechanisms, causing either amplification or damping of temporal and spatial variation, depending on conditions.

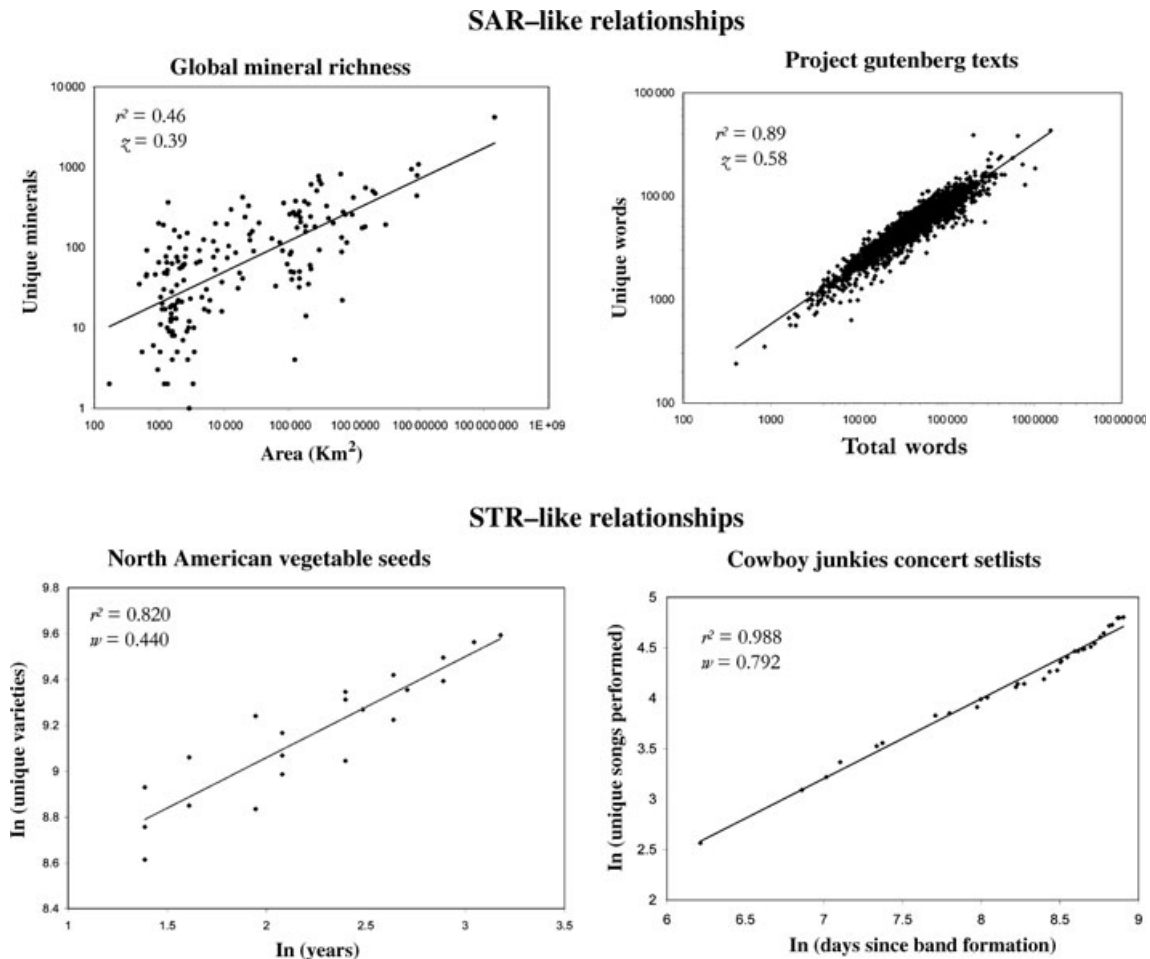


Figure 2 Species–area relationship and species–time relationship analogues for non-ecological systems, including the accumulation of unique mineral varieties by sample area, unique words by total document words, and unique vegetable varieties and Cowboy Junkies songs by time. All data are graphed on log-transformed axes. Best-fit linear regression lines have been plotted for each relationship.

- (6) They are open systems which require exchanges of energy, materials, and/or information from extrinsic sources to maintain highly organized states far from thermodynamic equilibrium.
- (7) They are historically contingent, so that their present configurations reflect the influence of initial conditions and subsequent perturbations.
- (8) They are often nested within other complex systems, giving rise to hierarchical organizations that can be approximated by fractal geometry and dynamic scaling laws.

Ecological communities clearly demonstrate these features. Even the simplest contain thousands to billions of individuals of tens to thousands of different species, ranging from unicellular prokaryotes, protists, and fungi to multicellular plants and animals. These individuals and species interact with each other and their extrinsic abiotic

environment across multiple spatial and temporal scales. These relationships are often inherently nonlinear, ranging from Michaelis–Menten curves for nutrient uptake to exponential or logistic population growth to the normal, skewed or bimodal distribution of species along environmental gradients. Feedbacks are prevalent, as demonstrated by effects of keystone species on ecosystem function or fuel buildup on fire return frequencies. Ecological communities require the continual transformation of energy, material and information to maintain their highly organized, far-from-equilibrium thermodynamic states. Many ecological processes are historically contingent, with contemporaneous patterns reflecting legacies of past events in both shallow (e.g. the sequence of habitat colonization) and deep (e.g. plate tectonics and evolution) time. And finally, ecological communities are composed of nested hierarchies of complex components, ranging from organic

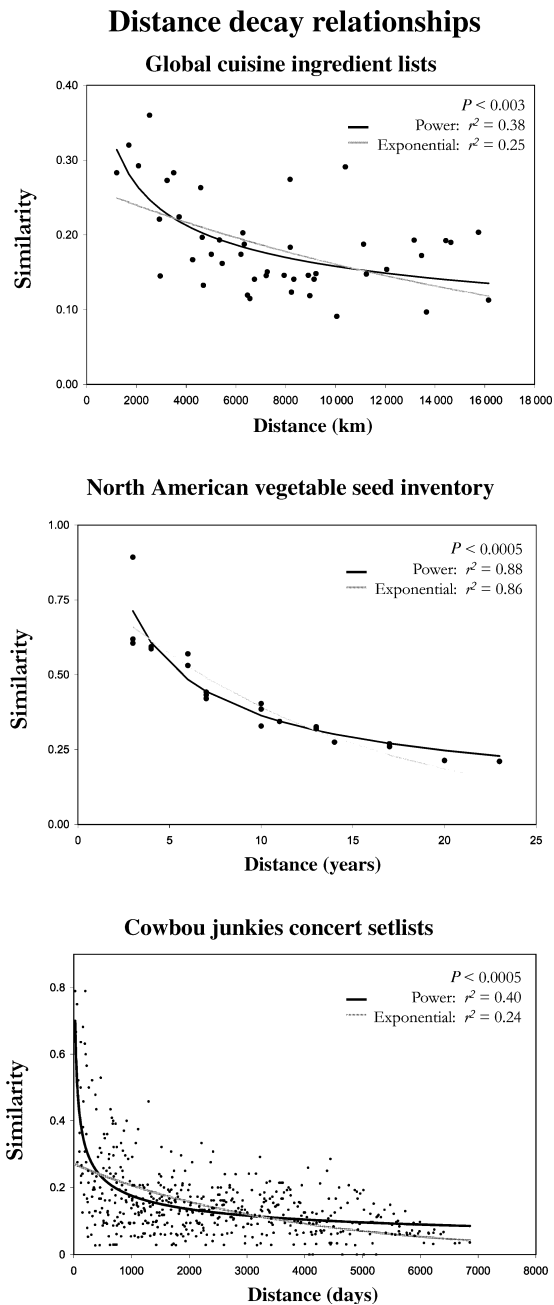


Figure 3 Distance decay analogues for non-ecological systems, including the change of compositional similarity of global cuisine ingredient lists over space, and garden seed offerings and Cowboy Junkies song performances over time. Best-fit exponential and power law decay lines have been plotted for each relationship.

molecules and cells through populations, species, guilds and trophic levels.

Because of these shared structural and dynamical properties, ecological communities and other kinds of complex systems tend to develop similar patterns of

whole-system structure and dynamics. An example of this is the occurrence of many small and few large magnitude events, which can be observed in the cumulative frequency distributions of word use, scientific paper citations, Internet web hits, copies of books sold, telephone calls received on a single day, earthquake magnitudes, lunar crater diameters, solar flare intensity, deaths in wars, wealth of rich people, surname frequencies, and city populations (Newman 2005). These patterns can often be nearly equally well fit by power law or log-normal probability distribution functions (West & Shlesinger 1989). The finding of DOW analogues (rarity-enriched SADs, roughly power law SAR and STR, and nonlinear DD) across multiple non-ecological systems thus suggests that these patterns represent shared statistical properties of a large class of complex systems. To discover the 'law' sought by Preston to explain these striking convergences may therefore require an understanding of the general principles that govern the structure and dynamics of all these systems.

The uncanny similarity of ecological DOWs to those exhibited by other complex systems has been largely ignored by community ecologists, who for the most part have sought explanation strictly from biological processes (but see Limpert *et al.* 2001; McGill 2003b; Halloy & Whigham 2004; Ugland *et al.* 2005). A few authors have pointed out phenomenological similarities between ecological and other complex systems and suggested that these may hold clues to common causes (e.g. Preston 1950, 1981; May 1975, 1981; Bak *et al.* 1987; Brown 1994b; Brown *et al.* 2000, 2002; Allen & Holling 2002; Solé & Bascompte 2006), but others have suggested that such similarities are spurious (Root 1989). Until such convergences are taken seriously and efforts are made to identify their root causes, community ecology risks becoming a myopic enterprise.

There are, in fact, a number of general processes that might influence wealth accumulation across a wide variety of systems. First, and perhaps most importantly, log-normal and mathematically related power law probability distributions are easily generated by the multiplicative rather than additive interaction of variables. Such processes have been shown to commonly apply to many physical (Meijer *et al.* 1981), biological (May 1975; McGill 2003b) and human systems (Montroll & Shlesinger 1982). Even the log-normal distribution of publication rates for researchers within scientific institutions is governed by such multiplicative processes (Shockley 1957). Similar distributions may also be generated by the interaction of multiple agents governed by nonlinear processes (Bak *et al.* 1987; West & Shlesinger 1989). Because of these processes, rarity-enriched SAD analogues may be a universal expectation for many complex systems (McGill 2003b). Second, many physical, biological and human systems exist within environments that exhibit power law or fractal-like spatial and temporal variation

(Mandelbrot 1982; Milne 1991; Ritchie & Olff 1999; Brown *et al.* 2002). Not only can these environmental templates be generated via simple hierarchical random models (Sizling & Storch *in press*), but can also in turn give rise to typical DOW patterns such as the power law SAR and nonlinear DD (Sizling & Storch 2004; Harte *et al.* 2005). Third, proximity effects, which occur when the influence of an event on an agent is dependent upon the distance in space and/or time between agent and event, occur in many physical, biological and human systems. Such relationships may be found across phenomena as diverse as electromagnetic radiation and gravitation to natural disturbances, dispersal and diffusion to migration, trade and wars. Proximity effects not only can directly give rise to DD relationships (Nekola & White 1999), but also can be an important source of multiplicative relationships over space or time. It is also possible to identify direct analogues in the processes governing different systems. For instance, both ecological and human systems exhibit hierarchical arrangements of agents, including individuals within populations and soldiers within armies and specialized classes of workers within insect societies and manufacturing firms. The structures and dynamics of both ecological and human systems also reflect a complicated dynamic balance among diverse cohesive and divisive forces, such as mutualism, reciprocity, and cooperation on the one hand and self-interest, competition, and predatory or parasitic exploitation on the other. The joint effects of such factors conspire to ensure that 'wealth' is distributed highly unequally among agents and nonlinearly over space or time.

What lessons can be learned from viewing ecological communities as complex systems and ecological DOWs as shared statistical properties of such systems? First, the mechanistic explanation for many of ecology's most venerable statistical patterns lie at a level of abstraction extending far beyond the realm of ecological process. The paradox that rarity-enriched SADs, power law SAR/STR, and nonlinear DD are generated by models assuming either complete neutrality or resource competition is therefore explained by realizing both models generate dynamical complexity. In competition models complexity arises as multiple agents, each with individualistic resource utilization and dispersal functions, interact in an elaborate network with multiple other agents often over multiple temporal and spatial scales. Such interactions can be made even more complicated and realistic by inclusion of some degree of stochasticity in resource requirements and dispersal processes (Tilman 2004). In neutral models complexity arises as multiple agents, each with a unique community and metacommunity frequency, undergo a lottery for recruitment of vacated spaces. These interactions are further complicated as new species are supplied to the system across multiple scales via dispersal and speciation. As a result it

may prove impossible to infer underlying mechanisms from DOW mathematical forms, both in general and for specific cases. However, this should not suggest that efforts to adduce ecological community assembly mechanisms must be abandoned. For instance, while a power law relationship describes the relationship between mean and variance for heartbeat frequency or interstride interval, the slope of this function supplies information about the relative importance of deterministic vs. stochastic drivers (West & Latka 2005; West 2006b). Similar mechanistic inferences can be made in ecological systems. In the case of the SAR, it has long been recognized that differences in slope over local-to-global scales or between islands and mainlands convey information about the mechanisms that generate and maintain diversity (Rosenzweig 1995). Similarly, DD rates provide information about niche characteristics and dispersal capacities in relation to the environmental template of spatial and temporal variations. So, for example, isolated spruce-fir forests of the Appalachians demonstrate an almost threefold greater DD rate when compared with continuous northern Taiga, and large-fruited, more dispersal-limited plant species have almost twice the DD rate when compared with smaller-seeded taxa (Nekola & White 1999).

Second, we question the utility of investing great effort to determine whether competition or neutrality might be responsible for observed DOWs when there is no logical reason to expect these mechanisms to be mutually exclusive – or, for that matter, to represent the only possible alternatives. Such patterns are almost certainly generated by combinations of stochastic and deterministic processes, local and regional processes, current and historical events, biotic interactions and abiotic factors, direct and indirect interactions, and cohesive and divisive forces. Similarly, diverse combinations of factors likely generate analogous properties in some physical and many human social and economic systems.

Third, it is long overdue that community ecologists keep abreast of developments in the field of complexity science. We are not suggesting that complexity science has all the solutions to the big important questions of community ecology. Indeed, complexity science is struggling to address similar problems and can currently offer few definitive answers. However, we are suggesting that ecological, physical and social scientists have much to learn from each other. Ideas, models and data from community ecology have the potential to make important contributions to complexity science, just as theoretical and empirical advances in complexity science have the potential to enlighten community ecology. This focus on interdisciplinarity is not a revolutionary concept. Community ecology has a long tradition of borrowing ideas and techniques from many other fields including economics (e.g. law of supply and demand, MacArthur & Wilson 1967; game theory, Smith 1982; Gini coefficients, Weiner & Solbrig 1984; supply side

ecology, Roughgarden *et al.* 1987), geography (DD, Nekola & White 1999; gravity models, Bossenbroek *et al.* 2001); the behavioural sciences (e.g. multidimensional scaling ordination, Minchin 1987), and physics (e.g. diffusion models, Skellam 1951; chaos, May 1976; percolation theory, O'Neill *et al.* 1992).

Finally, complexity science suggests that certain aspects of community ecology may never be highly predictable. While qualitative forecasts may be possible, the precise quantitative prediction of individual events may pose insurmountable challenges. For example, while it might be possible to predict qualitatively how community-wide SADs and SARs will be altered by invasions of multiple exotic species, it will be much more difficult to exactly predict resultant species abundances and spatial distributions. Indeed, such an effort may be as quixotic as attempting to predict the exact location of an electron in a shell or date and magnitude of the next earthquake in the San Francisco Bay area or price of General Motors stock in 2050. As in weather forecasting, some level of short-term predictability will often be possible from understanding current drivers, recent trajectories, and spatial/temporal autocorrelations. However, predictions based on these dynamics will necessarily become increasingly imprecise as the forecast period increases.

Rather than emphasizing prediction, community ecologists perhaps should spend more effort on understanding the mechanisms and events that have conspired to generate current and past patterns. Even when it may be practically impossible to predict the exact future trajectory of a system, by looking backward it may be possible to deduce quite accurately when and how specific mechanisms came into play. In complex human systems mechanisms are deduced by historians who analyse *post hoc* the particular combination of initial conditions and drivers that generated pattern. Similarly, community ecologists could enhance their understanding of the spatial and temporal patterns of biodiversity by becoming better natural historians, using *post hoc* analysis to decipher how past events have left lasting influences. By retrospectively studying systems, community ecologists may thus be able to establish what factors lead to the dominance of a particular taxon or to the occurrence of a particular hantavirus outbreak or simply whether Schrödinger's Cat survived.

For community ecology to continue making exciting advances, it must recognize that the distribution of abundance among species has much in common with distributions of 'wealth' in many other non-ecological systems. The fact that the distribution of species abundance is very similar to the distribution of drinking glass longevities or Cowboy Junkies song performances is thus both empowering and humbling in equal parts. While such similarities suggest a possible unification between ecolog-

ical communities and other complex systems, they also suggest that many of ecology's cherished fundamental patterns may reflect general phenomena that have more in common with statistical physics than species biology. The apparent universality of the rarity-enriched SAD, power law SAR/STR, and nonlinear DD suggests that community ecologists should pay attention to these more fundamental levels of inquiry and explanation. Complexity researchers of all types, including community ecologists, would be well advised to follow Frank Preston's path and to focus on the common factors that underlie these seemingly ubiquitous distributions of wealth.

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