

# Chapter 1: Universality in Ecology

*I see universal patterns. They're everywhere.*

The documentation of biodiversity, and determination of its underlying mechanisms, are among the most investigated topics within the field of ecology. Such inquiries have also become foundational to humanity's efforts to maintain that diversity. And yet, perhaps surprisingly, many of the patterns used in these analyses are shared with other seemingly unrelated areas of inquiry such as geology, meteorology, astronomy, economics, computer science, sociology, linguistics, and the arts. As early as 1950 Frank Preston commented on the remarkable similarities between the Boltzmann frequency distribution of kinetic energies in gas particles, the Pareto frequency distribution in personal incomes, and the frequency distribution of species abundances in ecological communities. Within the context of complexity science and statistical mechanics such cross-disciplinary patterns have been referred to as expressing 'universality'. However, outside of a few visionary thinkers (like Frank Preston), ecologists have been slow to identify universality within their midst, let alone to consider their potential ultimate causes and implications for inferential deduction.

The following book is intended to fill this gap. Its major goals are to:

- (1) *Document the presence of universal pattern within ecology and explain why it exists.* We will provide a background into the study of universality, enumerate and categorize universal patterns within ecology, and consider their underlying mechanisms ranging from the trivial (data transformation) to profound (mathematical logic/geometry, statistical mechanics, and physical/chemical laws).
- (2) *Discuss the implications of universality for ecology.* Because they are shared with systems as divergent as astronomy and the arts it seems unlikely that the ultimate causes for these patterns have much to do with processes normally considered essential in ecological explanation such as competition, predation, selection, niche dynamics, recruitment, and migration. While it may be possible to cast these into a more general framework that is applicable across diverse fields, there may also be value in viewing ecological systems from non-ecological perspectives to determine whether phenomena unique to ecology are required for their generation.
- (3) *Incorporate a universality perspective into ecological inference.* We will consider how universal patterns should and should not be used to test ecological hypotheses, and illustrate how their misinterpretation has created profound confusion. We will show ways in which useful ecological information can in fact be recovered from them, and provide an approach that incorporates universality into the search for ecological process.

We conclude the book by detailing how the existence of universality makes a strong case for the study of idiosyncrasy and unique case studies, often negatively ascribed to as 'natural history'.

Our Journey Begins. This is an admittedly complicated story told at least partially from outside the normal confines of the ecological discipline. It has many twists and turns. So perhaps it's best to start with some relatively simple and well known examples firmly rooted in ecology. In particular, let's consider the species abundance distribution, species accumulation function and distance decay of similarity within a single iconic dataset collected from the tropical forest canopy at Barro Colorado Island (BCI), Panama. We then come to our first twist: these exact

same patterns not only also exist within concert playlists of the alternative rock bands Cowboy Junkies and Phish, but are characteristic of many other datasets spanning an incredible range of systems.

*The Species Abundance Distribution (SAD)* describes the distribution of individual abundances across all species within an assemblage. A common way to visualize this data is through histograms in which bin widths are logarithmically scaled. Preston (1948) advocated the use of a doubling rule (which he termed octave-binning) in which each bin contains twice the abundance range as that immediately preceding. Across almost all ecological systems the SAD displayed using such logarithmic binning exhibits a normal-like curve (e.g. Preston 1948, 1962). This is clearly seen in canopy tree species abundances within 50 ha of tropical forest at BCI, with the distribution being generally bell-shaped and centered on a mode occurring between 32 and 64 individuals/species (Figure 1). However, SAD curves are rarely symmetrical, with the bins representing the rarest species almost always being more populated than those representing the most common. For BCI forest, the three left bins representing the rarest species (1-7 individuals) contain more than twice the number of species as compared to the right three representing the most common (512-4097 individuals).

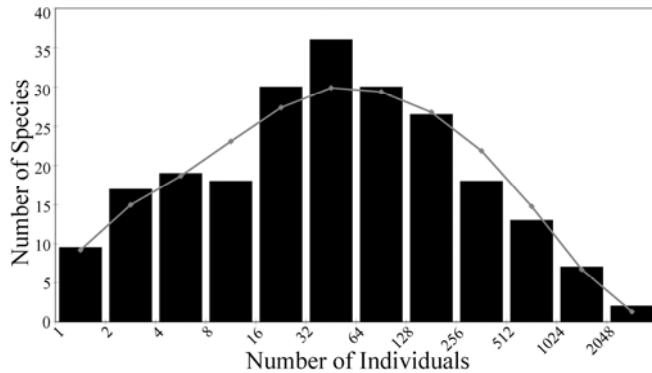


Figure 1: Abundance of canopy tree species from a 50 ha plot in closed canopy forest at BCI, presented as a histogram using the octave-binning rules of Preston (1948). The grey line represents the best parameterization of the ZSM distribution with  $\theta=50$  and  $m=0.1$  (after Hubbell 2001).

Figure 1 shows a histogram of species abundances with a grey line representing the best parameterization of the ZSM distribution. The distribution is bell-shaped and centered on a mode occurring between 32 and 64 individuals/species. However, SAD curves are rarely symmetrical, with the bins representing the rarest species almost always being more populated than those representing the most common.

For BCI forest, the three left bins representing the rarest species (1-7 individuals) contain more than twice the number of species as compared to the right three representing the most common (512-4097 individuals).

Preston (1948) saw this asymmetry as being related to truncation of a lognormal distribution to the left of 1. This must happen given that species abundances can only be quantized into full integers: fractional individuals cannot exist in real ecological communities. Thus, any species not represented by at least a single quantized individual in a particular sample will not be included in the distribution, even though they might be part of the larger species pool. Preston referred to this lower observed abundance bound as a ‘sampling veil’, and showed that its position was related in large part to the interplay between the underlying abundance distribution and sampling intensity, with the veil creeping closer and closer to (or even surpassing) the modal abundance class as the number of sampled individuals decreases and the relative proportion of rare species increases.

Hubbell (2001), however, believed that rare species enrichment could not be explained solely via this mechanism. Rather, he saw the presence of a long left-tale that made the distribution fundamentally asymmetric around the mean, beyond that generated by the  $n=1$  veil line. To accommodate this he created a new statistical distribution termed the Zero-Sum Multinomial (ZSM). Its shape was generated through a neutral community assembly model that (in general terms) assumes random replacement of open spaces by individuals/propagules from the surrounding species pool, with each species in this pool having identical traits. The model

limited establishment to vacancies created by the removal of pre-existing individuals. Thus, the total number of individuals – independent of species identity – remained constant. This distribution was parameterized based on two free variables: a dimensionless universal biodiversity number ( $\theta$ ) and migration rate ( $m$ ).

Sorting between these competing hypotheses has proven extremely difficult (e.g., McGill 2003, Volkov et al. 2003, Chave 2004, Etienne & Olff 2005) in large part because there is typically not enough statistical power within ecological datasets to allow for unambiguous model selection.

*Species Accumulation Functions (SAFs)* represent a constellation of relationships that document how species richness increases with increasing sample size / observation scale, with the various types differing based upon what aspect of ‘sample size’ is being considered: the Species-Individual Relationship (SIR; also known as the Collectors’ Curve) documents species accumulation with the increase of encountered individuals; the Species-Area Relationship (SAR) documents species accumulation with increasing sample area, while the Species-Time Relationship (STR) documents species accumulation with the increase of elapsed time over which observations were made. In terms of the SAR (and to a lesser extent the STR) increasing sample area can be decomposed into grain and extent, with the former representing increased quadrat size and the latter increased sample dispersion. While increasing sample grain must also increase its extent to some degree, sampling protocols that maximize the extent component by spreading uniform quadrats across large extents will encounter new species at the highest rate (Palmer & White 1994).

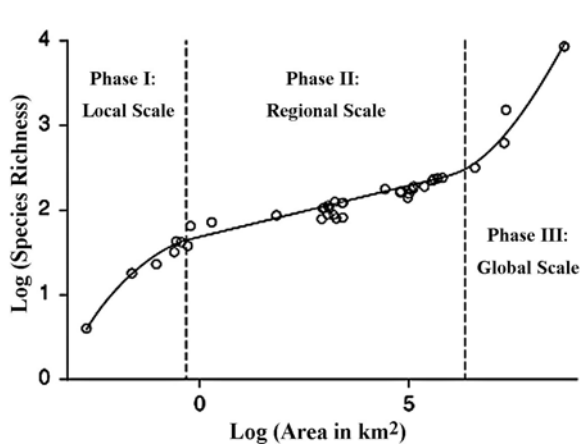


Figure 2: Tri-phasic SAR for birds, starting with individual small woodlots in western Pennsylvania and extending across the nearctic to the entire globe. Adapted from Preston (1960).

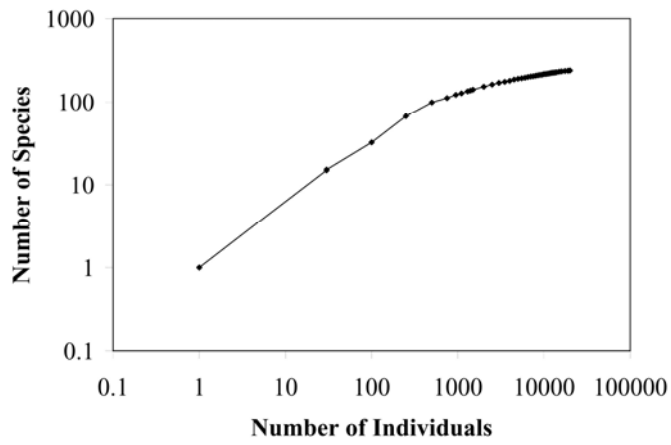


Figure 3: SIR for trees >10cm dbh in the 50 ha BCI plot. Species richness was calculated by averaging richness across randomly chosen areas (after Fig 6.9 of Hubbell 2001).

No matter the specific form being analyzed, SAFs generally exhibit a positive decelerating shape with increasing sample size. For the SAR both power-law (Arrhenius 1921) and logarithmic (Gleason 1922) forms have been variously advocated. Identification of which best explains a given ecological dataset has again proven difficult (Loehle 1990, White et al. 2006) for the exact same reason as seen in the SAD: there is often not enough statistical power to allow definitive selection between competing models (May 1975, Connor & McCoy 1979).

After review of the available data, Preston (1960, 1962) made a case for the power-law form as the general expectation. He also suggested that the SAR/STR pattern was tri-phasic (Figure 2), being initially steep as new species were encountered at a more rapid rate due to more complete sampling at local scales, and again at the largest spatial scales due to rapid turnover of species across major biogeographic barriers. At BCI, observed SIR (Figure 3) demonstrates a bi-phasic power-law form, with a more rapid increase of unique species up to around 1000 individuals, after which the slope shallows. It seems likely that this is related to the transition between Phase I and Phase II in the SAR.

*The Distance Decay of Similarity*

(DD) documents the non-linear decelerating decrease of compositional similarity with increasing intersample distance, whether in space, time, or environment (Nekola & White 1999). Its functional form is scale dependent, with power-law decay being characteristic within and exponential decay between communities (Nekola & McGill 2014). Perhaps the first illustration of this relationship – in any field – was by Preston (1962) who demonstrated the exponential decay of similarity between the vascular plant floras of islands in the Galapagos archipelago. This pattern is ubiquitous across most ecological systems, including tropical forest canopy in the Panama Canal area (Figure 4). In this system non-linear decay is apparent both within the 50 ha BCI sample plot (distances <2 km), and across the entire region (up to 110 km). While adjacent subplots within the 50 ha BCI quadrat may possess similarities up to 0.7, maximum similarity values fall to 0.1 or less when plots are separated by 70 km or more.

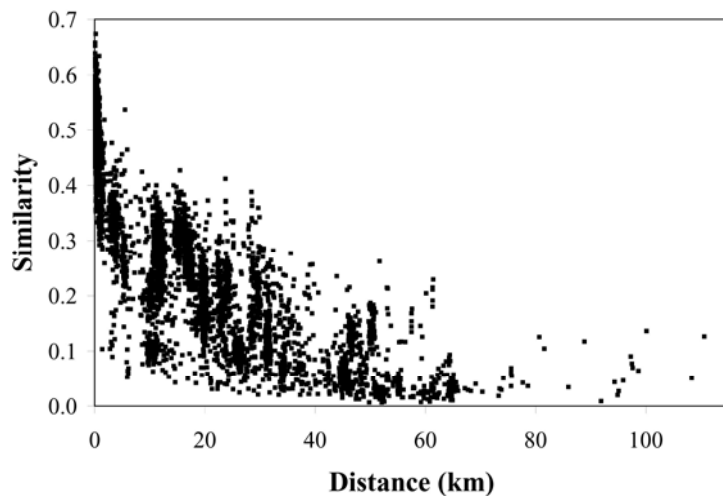


Figure 4: Distance decay of tropical canopy forest Jaccard similarity for 100 1ha quadrats across Panama, based on data presented in Condit et al. (2002). Most of the intersample distances <2km represent subsamples collected within the main 50 ha BCI quadrat.

Hubbell (2001) made the case for neutral community assembly by showing that his model readily generated the stereotypic shapes of these three patterns at BCI (as well as other ecological datasets): the ZSM distribution well fits to the observed SAD at  $\theta=50$  and  $m=0.1$ ; the power-law nature of the SIR/SAR can be generated through neutral community assembly; and the non-linear decreasing decelerating shape of DD is also an expected outcome of neutral replacement process. Based on this he then asked the question: why should niche-driven competition be assumed as the sole driving force in community assembly when – at least from the perspective of these three metrics – it is apparently not required?

Enter the Cowboy Junkies. But are these phenomena uniquely ecological? Could something larger be at play? This question had its inception while listening to the Cowboy Junkies. Formed in 1985 by Alan Anton (bassist) and siblings Michael (songwriter, guitarist, and

occasional vocalist), Peter (drummer) and Margo (vocalist) Timmins, the band’s first public performance occurred in 1986 at the Beverley Tavern on Toronto’s Queen Street West. Over their 30-year (and counting) existence, The Cowboy Junkies have recorded a total of sixteen studio and five live albums. Their unique mix of blues, country, folk, rock and jazz have earned them both critical acclaim and a loyal fan base.

In many ways Cowboy Junkies concert setlist data (as well as those from other bands) corresponds well to that from ecological communities: each concert can be seen as being equivalent to a sample quadrat within which a number of discrete performances (the equivalent of individuals) occurs. Each performance can be assigned to a particular song (the equivalent of a species). The total number of unique songs in a concert is then comparable to species richness (alpha-diversity), with the replacement of songs across concerts being comparable to compositional turnover (beta-diversity). The temporal distance between concerts can be determined just as can the spatial or temporal distances between ecological observations.

How do SAD, SIR, and DD patterns of Cowboy Junkies setlists appear when treated in the same way as ecological data? To investigate this a series of 33 roughly equally-spaced concert setlists was assembled using data housed on the setlist.com website, beginning with the May 15, 1987 performance at Club Flamingo in Halifax, Nova Scotia and ending with the February 20, 2006 concert at the Lensic Performing Arts Center in Santa Fe, New Mexico. Over the course of this roughly 6500 day temporal extent these concerts contained 122 unique songs, with individual setlists ranging between 13 and 22 songs. The most commonly preformed song was “Misguided Angel” (being played at 25 concerts), while 28 songs were singletons and only performed once.

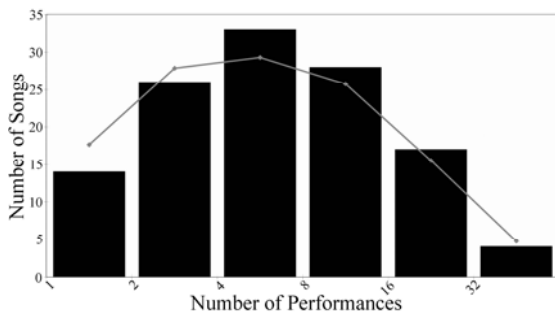


Figure 5: Song performance abundances across 33 Cowboy Junkies concerts from 1987-2006. The grey line represents the best fit zero-sum multinomial distribution with  $\theta=89.4$  and  $m=0.2$  (after Nekola & Brown 2007).

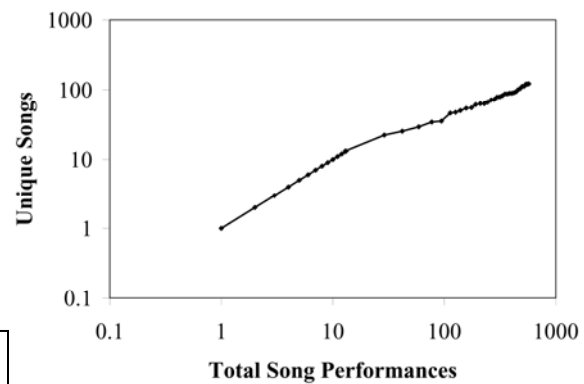


Figure 6: Unique vs. total song performances for 33 Cowboy Junkies concerts from 1987-2006.

Using the octave-binning rules of Preston (1948), song performance distribution (the setlist analog to an SAD) for Cowboy Junkies concerts demonstrate the same rarity-enriched lognormal-like shape as BCI, with the least performed songs making up the left-most two bins representing twice the number of songs as the right two bins. The ZSM distribution can be fit to these data at least as well as it could to BCI forest (Figure 5). The accumulation of unique songs (the setlist analog to the SIR) possess an almost identical shape to that seen at BCI, being a bi-phasic power law function with an initial steeper and subsequent shallower slope (Figure 6). In the case of Cowboy Junkies concerts, this transition corresponds to the accumulation curves found within vs. between concerts: as the 13 songs from the initial Club Flamingo concert were

constrained to have no repeats, it is not until multiple concerts are considered that repeated performances of the same song are possible and the accumulation curve becomes sublinear. In terms of DD, Cowboy Junkies setlists again show an analogous pattern to BCI, with similarity decaying non-linearly over time (Figure 7). While adjacent concerts possess a maximum song performance similarity of 0.8, this value fell to 0.1 or less beyond 6000 days. The main difference noted between these systems is that while Cowboy Junkies concert DD is best fit via a power law form over its entire domain, for Panamanian tropical forest DD form changes from power-law at small (e.g. <2 km) to exponential at larger scales (Nekola & McGill 2014).

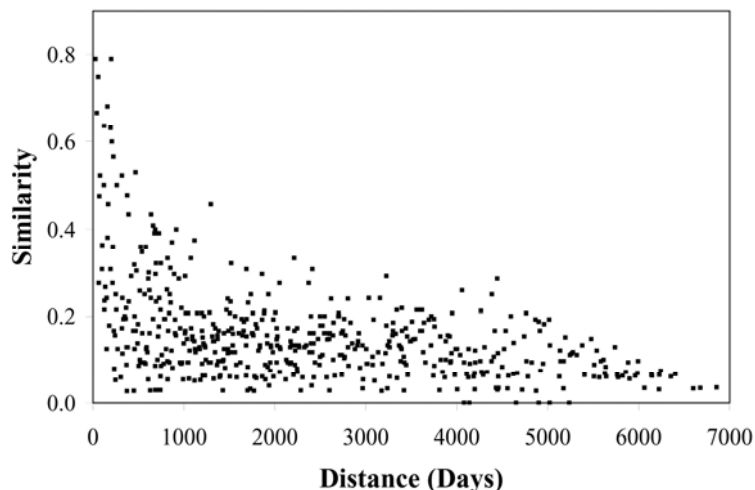


Figure 7: Distance decay of setlist similarity for Cowboy Junkies concerts. After Nekola & Brown 2007.

Thus, at least for the SAD, SIR, and DD, Cowboy Junkies concerts appear to be a close analog to BCI canopy forest: both display rarity-enriched abundance distributions that can be accurately summarized using a ZSM distribution; both display bi-phasic power law accumulation of unique entities as observation size increased, with initial rates being steeper and then becoming more shallow; both also display a non-linear distance decay of similarity, with power law decay being present at small scales. Does this mean that the process used by Alan Anton, Margo, Michael, and Peter Timmins to generate concert setlists mimics ecological community assembly? Or do these correspondences actually say more about the mathematical nature of these systems than the specific mechanisms operating within them?

Let's Go Phishing. To address this larger question, we must first determine if correspondence can be reproduced for other bands. Phish, formed at the University of Vermont in 1983 by guitarists Trey Anastasio and Jeff Holdsworth, bassist Mike Gordon, and drummer Jon Fishman, seemed an interesting contrast because of its dedicated fan base who would tour across the country with the band and attend every concert. As a result Phish assembled setlists to maintain considerable diversity between adjacent shows. Data was gathered from the Phististics website. For the SAD analysis, all 1195 concerts from 1983-2000 were included, representing a total of 22,738 song performances. These represented 674 unique songs. The most often performed was "You Enjoy Myself" (472 concerts) while 277 were performed only once. For SIR and DD analysis, one concert per year was selected, representing an extent of 6071 days. The 18 analyzed concerts captured 362 total song performances with 180 unique songs. The number of songs performed per concert ranged from 8 to 31.

Even given the different assembly rules which minimized overlap between concerts, Phish setlists again showed remarkable similarity to ecological communities (Figure 8): The SAD could be fit to a ZSM distribution with its octave-binned histogram displaying a very strong

enrichment in rare songs – the singleton and doubleton/triplet classes being five times more frequent than the two largest classes (256-472 performances). While admittedly not appearing as lognormal-like as BCI, the Phish setlist SAD does look similar to ecological assemblages which possess many very rare species and/or have been observed through limited sampling, such as stream diatoms (Patrick 1968) and moths attracted to light traps (Preston 1948). The SIR illustrated power-law accumulation, although with much less slope shallowing as compared to BCI or the Cowboy Junkies due to the greater turnover rate between concerts. And DD again illustrated a non-linear, power-law decrease across its entire domain. This relationship most differed from BCI and Cowboy Junkies concerts by its much lower maximum overlap between nearby concerts of  $<0.3$ .

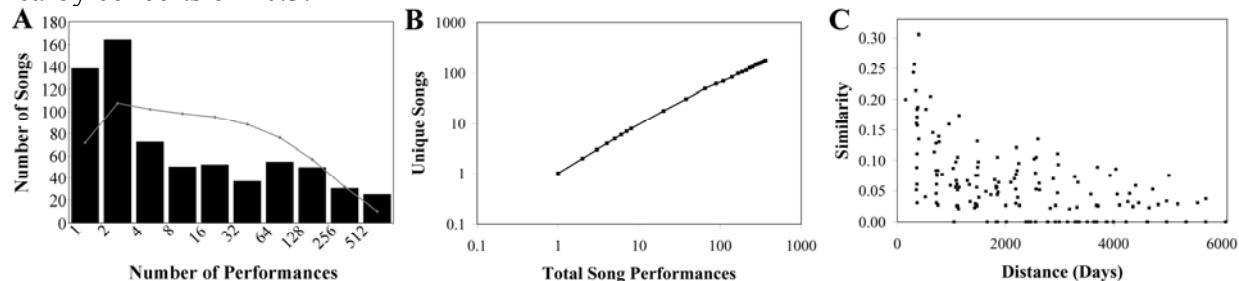


Figure 8: Analog community ecology metrics for Phish setlists. **A.** Octave-binned SAD for all concerts from 1983-2000. Illustrated curve represents the best fit parameterization of the zero-sum multinomial distribution with  $\theta=149.2$  and  $m=0.9$ . **B.** SID for 18 representative concerts. **C.** DD for 18 representative concerts.

Special Case or General Phenomenon? An obvious starting hypothesis to explain these correspondences is that band setlists mimic ecological communities at least in terms of their SAD, SAF, and DD shapes simply because of their analogous assembly rules, in which a given concert is created by selection of a roughly equivalent number of unique songs from a larger universe. But what happens if we relax assumptions further? Do these same basic patterns exist in systems where such processes are unlikely or not applicable? To do this the following datasets were compiled and analyzed:

**Physical Systems:** (1) Yearly precipitation averages in mm for each of the 1027 eastern North American land snail study sites reported by Nekola (2005), based on 1 km resolution global precipitation maps created by the WORLDCLIM Project; (2) Mineral species richness from county to global scales, as reported by the MINDAT database. Data represent the total number of minerals for the entire terrestrial globe, for ten countries (Australia, Canada, Chile, China, India, Mexico, Namibia, Turkey, United Kingdom, and USA), all US states (including the District of Columbia), all Canadian provinces/territories, and 2 counties per state.

**Economic Systems:** (1) 2004 Stock volumes for all publicly traded corporations in the USA, based on data reported by Bloomberg; (2) 2004 stock volume vs. number of companies within the 102 business categories reported by Bloomberg.

**Social Systems:** (1) Citation frequencies for all papers catalogued by the Institute for Scientific Information from 1981-1997; (2) The list of all commercially sold garden vegetable varieties in the US and Canada from 1981-2004 as reported by the Garden Seed Inventory of the Seed Savers Exchange; (3) The list of all ingredients reported in recipes for the cuisines of Ethiopia, Hungary, India, Iran, Ireland, Korea, Mexico, Norway, Puerto Rico, and Thailand from Smith (1990); (4) the number of occupied trailer homes per USA county in 2000 as reported in ESRI ArcView databases.

**Artistic Systems:** (1) The number of unique words and total word-length for the 1863 texts documented in Project Gutenberg as of 2000; (2) Word use frequency within the novel *Moby Dick* by Herman Melville.

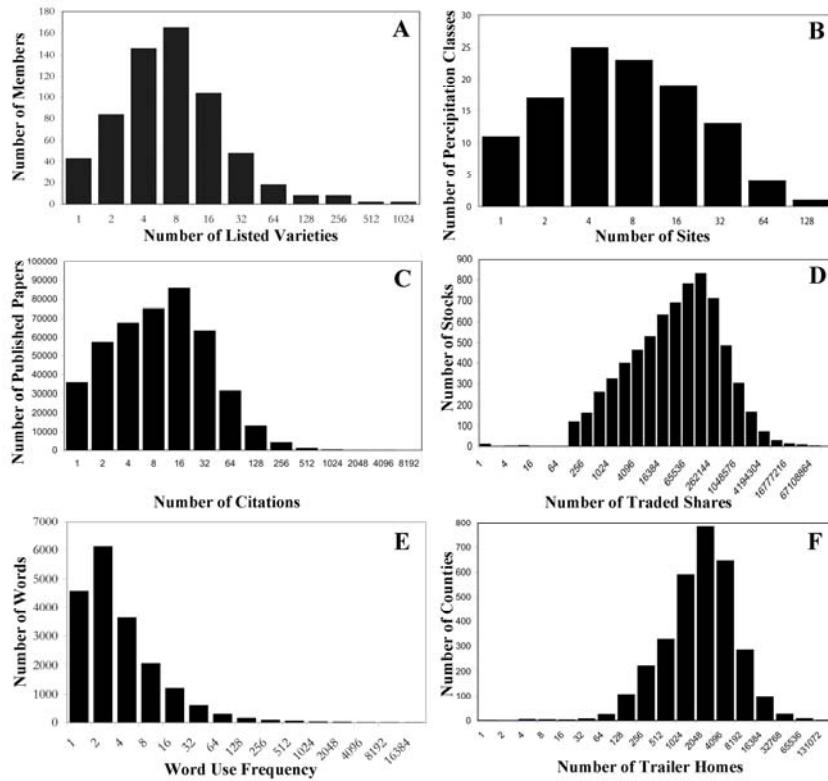


Figure 9: Analog SADs from various physical, social, and artistic systems using octave binning rules of Preston (1948). **A.** Number of vegetable varieties offered by each listed Seed Savers Exchange. **B.** Precipitation in mm classes across eastern North America. **C.** Citation frequencies for all papers catalogued by the Institute for Scientific Information. **D.** Stock volumes for all publicly traded corporations in the USA. **E.** Word use frequency in *Moby Dick*. **F.** Trailer home frequency per USA County.

For SAD analogs to exist, data within non-ecological systems had to be categorized into some type of identifiable units (SSE Members, mm precipitation classes; published scientific papers, stocks, unique words, counties) within which it was possible to count a discrete number of events (number of offered vegetable seed types; number of sample sites, number of citations, number of traded shares, word use frequency, number of trailer houses). While distribution shape varied across all six alternative systems, all shared a modal abundance class which was interior to the first and last bins (Figure 9). Many were similar to BCI in having the modal class occurring within the first 1/3-1/2 of total bin range (e.g. listed varieties by listed Seed Savers Exchange members, precipitation classes, citation frequencies). However, word use in *Moby Dick* was more like stream diatoms and Phish concert setlists with the sampling veil being within one bin of the modal abundance. All also demonstrated some form of rarity enrichment (Figure 9): in most cases this was seen by the left-most bins being more populated than the right-most (SSE member offerings; mm precipitation classes; scientific citations; word use) but could also represent a longer tail and slightly higher bin counts to the left of the mode than the right (trailer homes per USA county). Besides the Boltzman distribution of gas particle energies and the



Pareto distribution of personal incomes mentioned previously (Preston 1950), other examples of rarity enriched lognormal-like SADs from outside of ecology include the service life of restaurant drink tumblers, the static fatigue of glass and other materials, and first marriage age for Danish, UK, and USA women (Preston 1981). Because of their rarity enrichment, all these distributions would have been considered by Hubbell (2001) to possess something akin to a ZSM distribution. Because it is often not possible using conventional fitting routines to parameterize the ZSM for very large datasets (approximately  $>10^4$  events and/or categories), of the six examples in Figure 9 only the North American precipitation data could be fit. In this case the best-fit parameterization at  $\theta = 55.173$  and  $m = 0.179$  very closely matched observed frequencies. It should also be mentioned that stock volume data exhibits a sampling veil at 200 traded shares: the very few stocks sold at a lower annual volume are presumably eliminated from trading in the following year.

In terms of SAF analogs, all examples whether from physical (minerals), economic (number of companies), artistic (unique words), or social (garden seed richness) systems also demonstrated positive sublinear power-law relationships (Figure 10). Additionally, the accumulation of mineral types from county to global scales is arguably tri-phasic, being steepest up to about 100,000 hectares, and then again at the largest spatial scales. Other non-ecological examples of power-law accumulation have been recorded across time for comprehensive exam scores of degree candidates in the University of Oslo Department of Biology and quantized Norsk Hydro stock prices on the Norwegian market (Ugland et al. 2005).

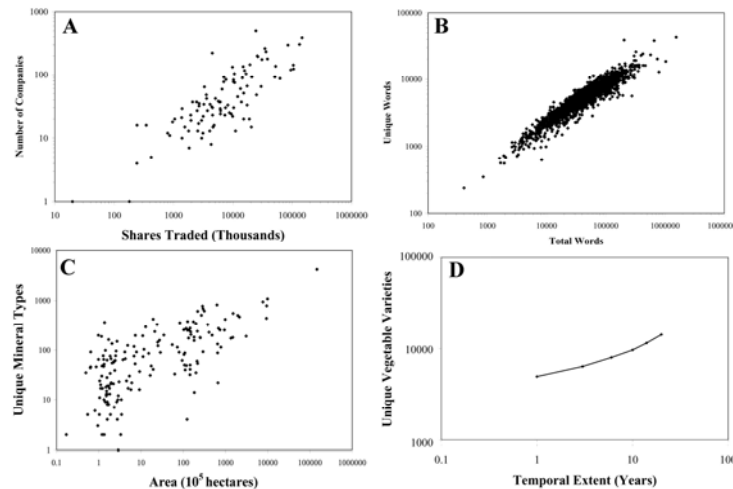


Figure 10: Analog SAFs plotted in log-log space. **A.** Number of companies vs. total stock volume. **B.** Unique words vs. total number of words in texts. **C.** Mineral richness vs. geographic area. **D.** Accumulation of unique vegetable varieties in the commercial North American trade from 1984-2004.

Non-linear DD was also observed (Figure 11) in social datasets across space (ingredient use in global cuisines) and time (commercial garden seed offerings). In both cases, a power-law decay form provides the best fit. Besides the two artistic setlist systems already shown to possess this same basic shape, physical and social systems are so replete with additional examples that the non-linear DD expectation has been codified as the ‘First Law of Geography’ (Tobler 1970).

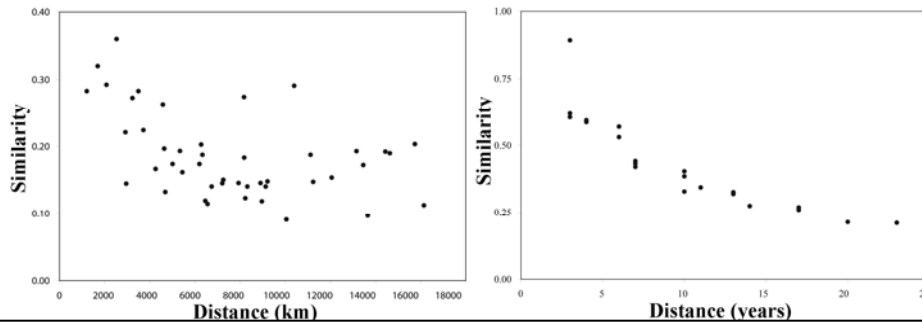


Figure 11: Analog DD relationships. **A.** Ingredients reported in recipes across ten global cuisines. **B.** All commercially available North American garden vegetable varieties 1981-2004

These examples illustrate that the replication of typical SAD, SAF, and DD forms is characteristic of systems spanning the physical and social sciences and the arts. Clearly the underlying reasons for these correspondences must lie beyond the confines of normal ecological mechanism.

The Ubiquity of Universality. Is universality simply limited to SAD, SAFs, and DD? Or is the phenomenon even more pervasive? To consider this, let's look at three other frequently analyzed macroecological relationships: the body size distribution, metabolic scaling, and abundance/density mapping.

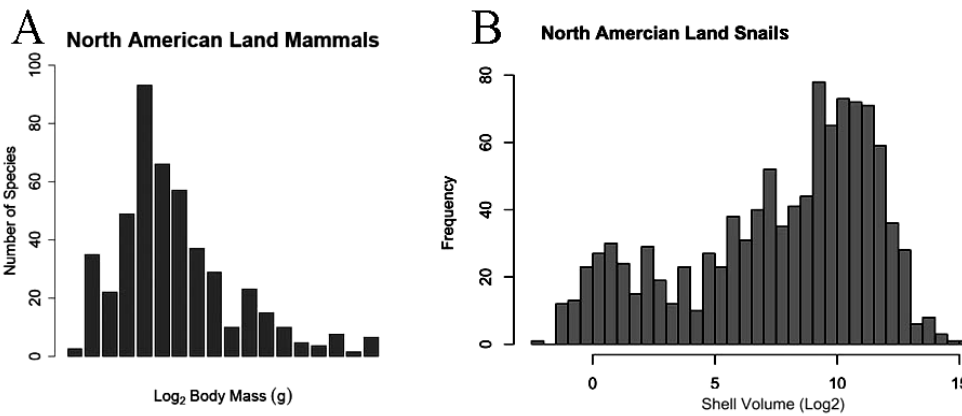


Figure 12: BSDs for North American Mammals (**A**) and Terrestrial Gastropods (**B**) using log<sub>2</sub>-transformed data. (modified from Brown & Nicoletto (1991) and Nekola (2014)). Note the bimodalism apparent in the land snail distribution.

*The Body Size Distribution (BSD)* was perhaps first analyzed by Hutchinson & MacArthur (1959) for various North American insects and mammals. In generating this distribution some component of body size (often maximum dimension, volume, or mass) is summarized across species. Typically the distribution is illustrated through histograms using log-transformed body sizes, often using base2. This makes the mathematics underlying BSD plots similar to that of octave-binned SAD histograms. Across most vertebrate groups, the BSD typically possesses a right-skewed lognormal shape (Figure 12A). While lognormality of the distribution appears consistent, the nature of skewing varies greatly, ranging from none to left-skewed (Figure 12B). Bimodalism can also be apparent (Figure 12B).

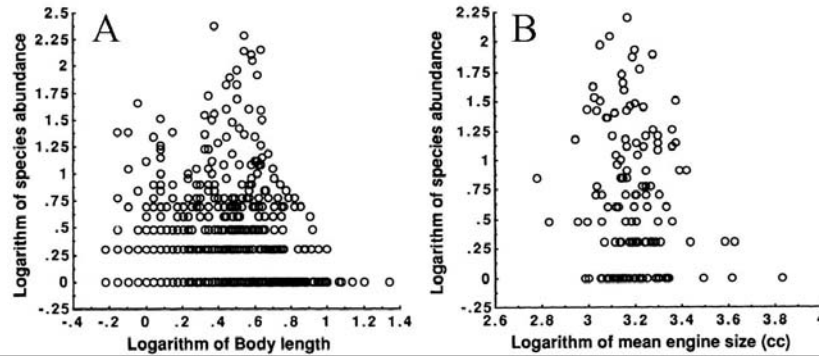


Figure 13: Abundance vs. body size for (A) Bornean lowland tropical forest canopy beetles and (B) vehicles at seven car parks in York, UK. Modified from Gaston et al. (1993).

Gaston et al. (1993) demonstrated using unbinned log-transformed data that the closely related body size vs. abundance distribution for Bornean tropical forest beetles was approximately right-skewed lognormal (Figure 13A). Using the same graphing method on a dataset of 1731 automobiles representing 147 different makes observed at seven car parks in York on January 4, 1989, a roughly similar right-skewed lognormal shape was generated (Figure 13B). Other correspondences also exist: For instance, Horn & May (1977) illustrated similarities in the linear dimensions of potentially competing animals to that of musical instruments and children's toys. From this they concluded that general rules pertaining to the assembly of tool sets may be more at play than 'any biological peculiarities'.

*The  $\frac{3}{4}$  power-law scaling of individual metabolism vs. body mass* is another frequently reported ecological pattern. The initial formulation of this relationship (Kleiber 1932) showed for homeothermic vertebrates a power-law relationship with metabolic rate scaling to the  $\frac{3}{4}$  power of body mass across six orders of magnitude. Subsequent work illustrates this relationship holding across all eukaryotic biological organisms, an astonishing size range of 18 orders of magnitude (Figure 14A). West et al. (1997) were able to mathematically derive the  $\frac{3}{4}$  scaling coefficient through minimization of the energy/time required to distribute resources in organisms possessing a space-filling fractal-like closed circulatory system with invariant terminal units. While the underlying assumptions of their model clearly applies to vertebrates and vascular plants, the  $\frac{3}{4}$  scaling coefficient also holds for invertebrates possessing open circulatory systems. The same relationship is also present in the macroeconomic comparison of per capita GDP (an analog to organism mass) to per capita energy consumption (an analog to organism metabolic rate) across all nations (Figure 14B). Again, something more general than the mathematics of closed circulatory systems must be at play.

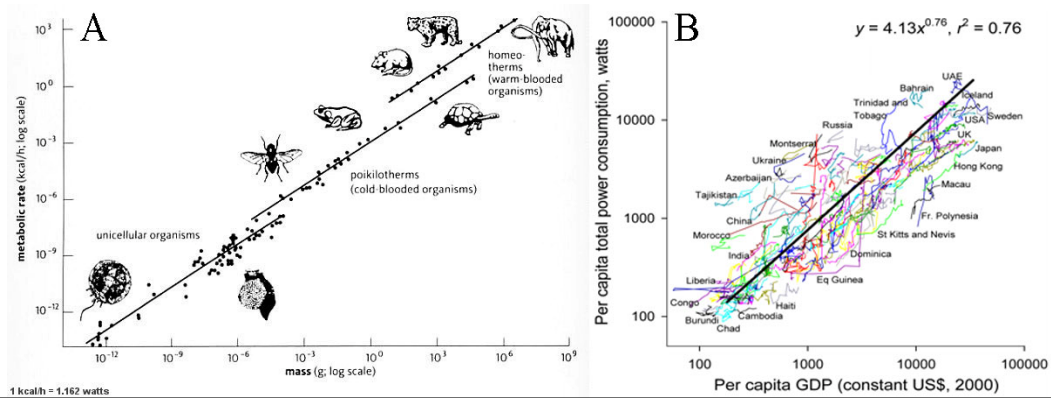


Figure 14:  $\frac{3}{4}$  power law scaling of mass vs. energy use for (A) animals (modified from Hemmingsen 1960) and (B) national economies (modified from Brown et al. 2010).

While consideration of how *species abundances map across two-dimensional space* goes back to at least Humboldt and Darwin, the empirical determination of these patterns based on high quality, large scale data has been limited to the past few decades. Thanks to resources like the North American Breeding Bird Survey and ready access to computer-assisted mapping, it is now possible to accurately display the empirical abundances of many species across multiple scales. Early researchers who did not have access to these data assumed that species abundances within a range would typically represent a normal, Gaussian curve, with a single abundance peak being found in the center of a range (e.g. Brown 1995). Empirical data suggests, however, that this is rarely the case. Rather it is typical for abundance: (1) to be multimodal with modes representing various sizes but with the largest being 2-3 orders of magnitude larger than the surrounding matrix; (2) to possess strong autocorrelation; (3) to have peaks make up a small proportion of the total range; and (4) to have peaks be scattered throughout the total range. McGill & Collins (2003) have summarized this as a ‘Peak and Tail’ abundance density pattern, and show that it may underlie much of macroecology. This is well illustrated for Coopers Hawk in North America (Figure 15A) which possesses at least a half-dozen scattered and non-centrally located high peaks (yellow color) across the USA and southern Canada, with many more small peaks being present. And at the same time, across most of its range the species is quite rare (dark red/black color). But is this pattern limited to ecology and biogeography? Again the answer is no: mapping of visible matter in the constellation Sextans by the Hubbel Space Telescope shows a pattern that matches all of the criteria for Peak and Tail species density patterns (Figure 15B). The abundance pattern for dark matter in this region of space is largely similar (Cosmic Evolution Survey, 2007). What possible factors and processes could be shared between the evolution of the Coopers Hawk range across North America and the distribution of matter across the universe?

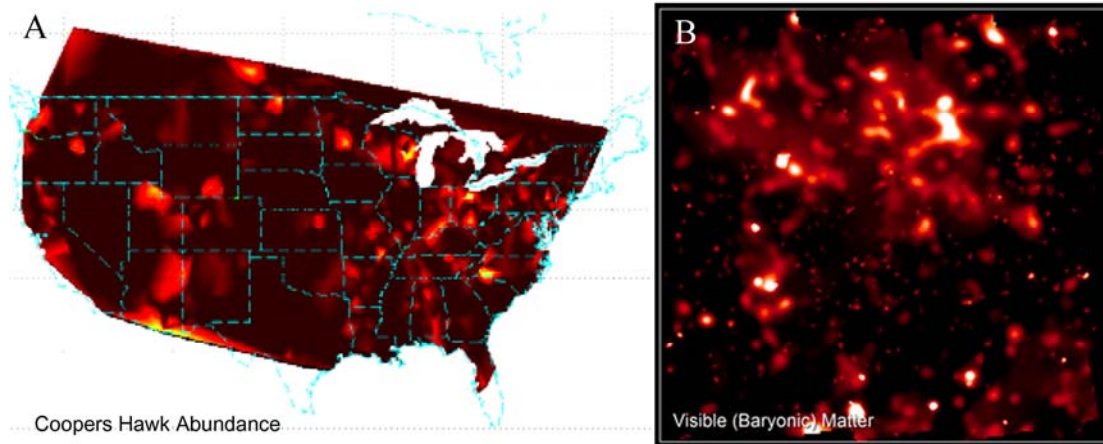


Figure 15: Density mapping of (A) Coopers Hawk abundances, based on the data from the North American Breeding Bird Survey (modified from McGill, *pers. comm.*) and (B) distribution of visible matter in 2x2 degrees of sky (modified from Cosmic Evolution Survey, 2007).

Additional cross-disciplinary correspondences likely exist. For instance, the frequency distribution of individual body size or energy use – independent of species – appears to largely represent a non-linear decelerating inverse function, perhaps of power-law form (Petchey & Belgrano 2010). Such decreasing power law frequency distributions are common across an incredible array of systems, including number of people killed in wars and terrorist events, personal net worth, surname frequency, city population size, hits per website, books sold, telephone calls received to a given number, earthquake magnitude, solar flare intensity, and lunar crater diameter (Newman 2005). A number of network metrics also likely apply across disciplines, in particular the non-linear decelerating (perhaps power-law) frequency distribution of the node count and network strength distributions, which exist not only for food webs but also across many social and physical networks.

Making Sense of These Congruences. Given the number of patterns and diversity of systems involved, how can they even be discussed let alone compared? One way to proceed is to look at general data structures which at least have a chance of being shared across a wide array of systems. The following should not be seen as an exhaustive list of all possible data attributes; they are simply some that appear useful in organizing the patterns previously discussed:

(1) *Is the system composed of discrete quantized entities?* These are usually referred to as ‘agents’ within the context of complexity science, and represent the smallest operative unit within a system. In ecology this often represents individuals. In setlists this is equivalent to each individual song performance. In word use analysis it is each individual word appearing in a text. In stock volume analysis it is each traded stock share. In citation analysis it is each catalogued citation.

(2) *Can these discrete entities be grouped into unique categories? Do the individual agents represent distinct forms?* For ecology this could represent the species to which individuals belong. For setlist analysis this would be the particular song to which an individual performance can be assigned. In word use it would be the unique word which is being used in a particular case. In stock volume analysis it would be the particular stock to which a given share represents. In citation analysis it would be the scientific paper which is being referenced.

(3) *What is the operational space/time window of a system? What is the observational lens through which entities/agents have been quantified?* In ecology this generally represents quadrat size and placement that defines a given dataset. In setlist analysis grain is equivalent to the length a single concert while extent represents the temporal spread of concerts.

(4) *Where are observations located? Where do the entities/agents occur?* In ecology this typically represents the geographic coordinates and/or date from which each observation/sample was taken. In setlist analysis this would be the temporal date of a given performance.

(5) *What is the size of an entity/agent?*

(6) *How much energy does an entity/agent contain/consume?* Note that both (5) and (6) can be analyzed not only at the entity/agent scale but also for the categories to which they belong. In these cases values must be statistically summarized in some way across entities within a given category.

(7) *What network information characterizes the linkage of entities/agents* such as the number of connections between or the amount of information/material transferred?

Using this framework, it is possible to cast universal patterns from ecology into a more general perspective (Table 1):

-The SAD is an example of the larger class of Category-Count Distributions (CCD) in which the number of discrete entities within all unique categories is determined. Ecological literature suggests that the CCD should take on a rarity-enriched lognormal-like shape (but we'll revisit this in Chapter 3).

-SAFs (SIR/SAR/STR) are all examples of a larger class of Category Accumulation Relationships (CAR) in which the number of unique encountered categories is compared to the number of individual entities, or amount of space or time which has been sampled. This relationship may represent a sublinear increasing power-law function, and possess varying slopes across the x-axis. Although CCDs and CARs differ in their focal pattern (entity abundance within categories vs. number of categories) they are based on fundamentally similar structures and can generally be produced from the same datasets. In fact, they (along with DD) may be accurately seen as different sides of the same multi-dimensional coin (e.g., He & Legendre 2002, McGill 2011, Chase & Knight 2013).

-Ecological DD is comparable to Distance Decay analyses in other fields. This pattern requires not only the presence of discrete entities within assignable categories, but also large enough individual sample sizes to allow for co-occurrence of entities representing multiple categories. It also requires that sample location be known so that intersample distances can be calculated. This relationship typically takes on some negative decelerating function, with both power law and exponential forms having been identified. It should also be mentioned that semi-variogram analysis is closely related and documents similarity decay within a single continuous (as opposed to discrete) variable.

-Size Distribution is part of a larger class of Entity-Size Distributions (ESD), in which entity size distribution is analyzed irrespective of assignable categories. These require the existence of discrete entities with measurable size/mass. This relationship appears to typically take a negative decelerating power-law form beyond some minimum-possible entity size dictated by system-specific conditions.

-The BSD is an example of the larger class of Category-Size Distributions (CSD) in which category frequency is analyzed across some statistical tendency of entity size across categories. This relationship may be lognormal-like in shape (again this will be revisited in

Chapter 3), with considerable expressed variability in the type and degree of skew and the number of modes.

-The Energy Distribution pattern is part of a larger class of Entity-Energy Distributions (EED), in which the energy content/use distribution is analyzed irrespective of categories to which the entities are assigned. These require the existence of discrete entities, with measurable energy use/content. This relationship appears to typically take a negative decelerating power-law form beyond some minimum-possible entity energy level which is dictated by system-specific conditions.

-Metabolic Scaling is an example of the larger class of Energy-Size Scaling (ESS) relationships, in which the central tendency of energy use/content of entities within given categories is compared to the central tendency of entity size within that category. The relationship appears to represent sublinear power-law accumulation with a coefficient of  $3/4$ . It should also be noted that this relationship appears part of an even larger class of trait vs. energy use power-law relationships that variously scale to quarter-powers, e.g.  $-1/4$ ,  $1/4$ ,  $1/2$ , or  $1$ .

-Ecological Density Mapping is comparable to that done in other disciplines, with entity abundance within a given category being mapped in space/time. It requires not only discrete entities assignable to unique categories, but also location coordinates for each entity. This pattern takes on a Peak and Tail shape.

-The Node Count Distribution applies to both ecological and non-ecological networks. It documents the number of other nodes connected to given node (entity) in a network, and appears to possess a non-linear, decelerating, decreasing shape, perhaps of power-law form. Depending upon the nature of the network, it can be based on either discrete entities or unique categories.

-The Network Strength Distribution also applies to both ecological and non-ecological networks. It measures the amount of energy/material/information transferred between nodes (entities), and also appears to possess a non-linear, decelerating, decreasing shape, perhaps of power-law form. It should be noted that these are just two of a multitude of network metrics that are analyzed and calculated, and that most of these are as applicable to ecological networks as they are to physical/social ones.

Table 1: Ten universal ecological patterns

Pattern Name in Ecology	Suggested cross-disciplinary name	Data elements							Expected shape
		Entities	Categories	Scale	Location	Size	Energy	Network	
Species Abundance Distribution (SAD)	Category-Count Distribution (CCD)	X	X	X					Rarity-enriched lognormal-like. While not needed to generate pattern, sample scale influences shape
Species Accumulation Relationship(SIR/SAR/STR/Collectors Curve)	Category-Accumulation Relationship (CAR)	X	X	X					Multi-phasic sublinear power law increase.

Distance Decay (DD)	Distance Decay	X	X	X	X				Non-linear decelerating decrease
Size distribution	Entity-Size Distribution (ESD)	X				X			Non-linear decelerating decrease
Body Size Distribution (BSD)	Category-Size Distribution (CSD)	X	X			X			Lognormal (normal or skewed)
Energy distribution	Entity-Energy Distribution (EED)	X					X		Non-linear decelerating decrease
Metabolic Scaling	Energy-Size Scaling (ESS)	X	X				X		Sublinear power law increase with $\frac{3}{4}$ coefficient
Density Mapping (DM)	Density Mapping	X	X		X				Peak and Tail abundance pattern
Node Count Distribution	Node-Count Distribution	X	X					X	Non-linear decelerating decrease
Network Strength Distribution	Network Strength Distribution	X	X				X	X	Non-linear decelerating decrease

The Path Ahead and Book Overview. Ecology thus appears replete with universal patterns shared across a vast array of other disciplines, and it is possible to organize these in a way to allow interdisciplinary comparison. What should we as ecologists make of this? What are their ultimate underlying mechanisms? What do they actually tell us about ecological process? Does their existence suggest that there may be less difference between ecological systems and their non-ecological counterparts than is typically acknowledged? How should it alter the way we look at and attempt to decipher the mechanisms underlying ecological pattern? And what do they imply about the importance of the search for generality vs. the identification of idiosyncrasy?

In Chapter 2 we overview the history of pattern universality investigation through the life and accomplishments of Frank Preston, who may well have been first scientist in any field to document universality at least 30 years before it was rediscovered by the complexity science community. In spite of this several of his most important works – and the ones that have inspired our interest in universality – went uncited for decades. This brief biography of Preston’s exploits will also serve as a historical overview of ecological universality and the ways in which this perspective has (and has not) been incorporated into ecological thought.

In Chapter 3 we demonstrate how mathematical transformation and poor choice of graphical representation – especially in terms of the SAD and BSD – creates an illusion of universality when in fact it does not exist. Such artifacts have led to profound confusion (and wasted effort) by incorrectly displaying the true nature of these patterns.



In Chapter 4 we show how mathematical and geometric logic, in particular the roles played by non-linear dynamics and dimensional scaling, constrain process and generate universality in systems of any size. We'll also discuss how the quantizing of continuous probability functions into discrete entities/events/agents likely underlies many universal patterns seen in biogeography and macroecology.

In Chapter 5 we extend mathematical logic to include systems made of a large number of entities. Such systems are constrained not only by basic probability theory (e.g. central limit theorem, Brownian motion, extreme value statistics) but also statistical mechanics. This latter field considers systems with a multitude of entities/agents, ignoring the specific details of each (microstate), instead making predictions about system emergent properties (macrostates) and/or their statistical distributions, and illustrates how these properties arise from the inherent uncertainty naturally embedded within the system. We provide an overview of the field, starting with the contributions of Bernoulli, Boltzmann, and Gibbs, then discuss entropy in the context of information theory as applied by Shannon, and conclude with Jaynes' grand unification of classical thermodynamics with entropy, probability theory and Bayesian logic.

In Chapter 6 we consider the simplest assumptions needed to reproduce ecological pattern, and show how a statistical mechanics approach may well contribute to the understanding of ecological communities.

In Chapter 7 we discuss a final suite of factors that can cause universality via the rules that govern the physical and chemical world, including the first and second laws of thermodynamics, fluid dynamics, friction, optics, and stoichiometric laws like the Redfield Ratio.

In Chapter 8 we move beyond the mechanisms generating universality to consider the implications these patterns have on ecological deduction. We show how the mere detection of universal pattern does not by itself allow for competing mechanistic hypotheses to be distinguished, and then illustrate how explicit ecological process can in fact be teased from universal patterns through analysis of functional form and parameterized coefficient values.

In Chapter 9 we step back to consider what 'mechanism' should mean in an ecological context when many of the patterns at the heart of the discipline are not limited to ecological systems. We propose a method to help identify the minimum number of mechanistic elements required to generate a given ecological pattern through a hierarchical arrangement of drivers from the most general (mathematical logic) to the most specific (processes limited expressly to ecology). We suggest that explicit disciplinary mechanism should only be invoked when more general processes fail to generate an observed pattern.

With Chapter 10 we finish this volume by taking an even further step back to consider the multiple viewpoints needed to advance ecological understanding. We argue that the more general the pattern, the more likely its ultimate cause will be anchored in mathematical logic, statistical mechanics, and/or various physical laws. So where should we look for pattern rooted purely in ecological mechanism? The answer may lie in the idiosyncrasies and 'just-so' stories of natural history. The job of an ecologist may thus be a theoretician and natural historian in equal measure, as there may be no other way to rectify the existence of universality with the truth that every square meter of the planet is biologically unique.

Through this work we hope to help bring pattern universality into the mainstream of ecological thought, and help ecologists (and hopefully complexity scientists, social scientists, physical scientists and others as well) become more thoughtful and productive in their use.

## References

- Arrhenius, O. 1921. Species and area. *Journal of Ecology*. 9:95-99.
- Brown, J.H. 1995. *Macroecology*. University of Chicago Press.
- Brown, J.H. & P.F. Nicoletto. 1991. Spatial scaling of species composition: body masses of North American land mammals. *American Naturalist*. 138:1478-1512.
- Brown, J.H., W.R. Burnside, A.D. Davidson, J.P. DeLong, W.C. Dunn, M.J. Hamilton, J.C. Nekola, J.G. Okie, N. Mercado-Silva, W.H. Woodruff & W. Zuo. 2011. Energetic Limits to Economic Growth. *Bioscience*. 61:19-26.
- Chase, J.M & T.M. Knight. 2013. Scale - dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters*. 16:17–26.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters*. 7: 241-253.
- Condit, R., N. Pitman, E.G. Leigh, Jr., J. Chave, J. Terborgh, R.B. Foster, P. Núñez V., S. Aguilar, R. Valencia, G. Villa, H.C. Muller-Landau, E. Losos & S.P. Hubbell. 2002. Beta-diversity in tropical forests. *Science*. 295:666-669.
- Conner, E.F. & E.D. McCoy. 1979. The statistics and biology of the species-area relationship. *American Naturalist*. 113:791-833.
- Cosmic Evolution Survey. 2007. <http://hubblesite.org/image/2034>
- Etienne, R.S. & H. Olf. 2005. Confronting different models of community structure to species-abundance data: a Bayesian model comparison. *Ecology Letters*. 8: 493-504.
- Gaston, K.J., Blackburn, T.M. & Lawton, J.H. 1993. Comparing animals and automobiles: a vehicle for understanding body size and abundance relationships in species assemblages? *Oikos*. 66:172-178.
- Gleason, H.A. 1922. On the relation between species and area. *Ecology*. 3:158-162.
- He, F. & P. Legendre. 2002. Species diversity patterns derived from species-area models. *Ecology*. 83:1185-1198.
- Hemmingsen, A.M. 1960. Energy metabolism as related to body size and respiratory surface, and its evolution. *Report of Steno Memorial Hospital (Copenhagen)*. 9:1-110.
- Horn, H & R.M. May. 1977. Limits to similarity among coexisting competitors. *Nature*. 270:660-661.
- Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Monographs in Population Biology #32. Princeton University Press.
- Hutchinson, G.E. & R.J. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. *American Naturalist*. 93:117-125.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia*. 6:315-353.
- May, R.M. 1975. Patterns of species abundance and diversity. In: *Ecology and Evolution of Communities* (eds. Cody, M.L. & J. Diamond). Harvard University Press, Cambridge, Massachusetts. pp. 81-120.
- McGill, B.J. 2003. A test of the unified neutral theory of biodiversity. *Nature*. 422:881-885.
- McGill, B.J. 2011. Linking biodiversity patterns by autocorrelated random sampling. *American Journal of Botany*. 98:481–502.
- McGill, B. & C. Collins. 2003. A unified theory for macroecology based on spatial patterns of abundance. *Evolutionary Ecology Research*. 5:469–492.
- Nekola, J.C. 2005. Geographic variation in richness, evenness, and shell size of eastern North American land snail communities. *Records of the Western Australian Museum*. Supplement 68:39-51.

- Nekola, J.C. 2014. Overview of the North American terrestrial gastropod fauna. *American Malacological Bulletin*. 32:225-235.
- Nekola, J.C. & J.H. Brown. 2007. The wealth of species: ecological communities, complex systems, and the legacy of Frank Preston. *Ecology Letters*. 10:188-196.
- Nekola, J.C. & B. McGill. 2014. Scale dependency in the functional form of the distance decay relationship. *Ecography*. 37:309-320.
- Nekola, J.C. & P.S. White. 1999. Distance decay of similarity in biogeography and ecology. *Journal of Biogeography*. 26:867-878.
- Newman, M.E.J. 2005. Power laws, Pareto distributions, and Zipf's law. *Contemporary Physics*. 46:323-351.
- Palmer, M.W. & P.S. White. 1994. Scale dependence and the species-area relationship. *American Naturalist*. 144:717-740.
- Patrick, R. 1968. The structure of diatom communities in similar ecological conditions. *The American Naturalist*. 102:173-183.
- Petchey, O.L. & A. Belgrano. 2010. Body-size distributions and size-spectra: universal indicators of ecological status? *Biology Letters*. DOI: 10.1098/rsbl.2010.0240
- Preston, F.W. 1948. The commonness, and rarity, of species. *Ecology*. 29:254-283.
- Preston, F.W. 1950. Gas laws and wealth laws. *Scientific Monthly*. 71:309-311.
- Preston, F.W. 1960. Time and space and the variation of species. *Ecology*. 41:611-627.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology*. 43:185-215, 410-432.
- Preston, F.W. 1981. Pseudo-lognormal distributions. *Ecology*. 62:355-364.
- Smith, J. 1990. *The Frugal Gourmet on Our Immigrant Ancestors*. Harper-Collins, New York.
- Tobler, W.R. 1970. A computer movie simulating urban growth in the Detroit region. *Economic Geography*. 46:234-240.
- Ugland, K.I., J.S. Gray & P.J. Lamshead. 2005. Species accumulation curves analysed by a class of null models discovered by Arrhenius. *Oikos*. 108: 263-274.
- Volkov, I, J.R. Banavar, S.P. Hubbell A. Maritan, A. 2003. Neutral theory and relative species abundance in ecology. *Nature*. 424:1035-1037.
- West, G.B., J.H. Brown & B.J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science*. 276:122-126.
- White, E.P., P.B. Adler, W.K. Lauenroth, R.A. Gill, D. Greenberg, D.M. Kaufman, A. Rassweiler, J.A. Rusak, M.D. Smith, J.R. Steinbeck, R.B. Waide & J. Yao. 2006. A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos*. 112:185-195.