

Implicit Scaling in Ecological Research

On when to make studies of mice and men

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Ecology focuses on tangible organisms; ecological complexity results from the myriad of patterns with which the many different types of organisms interact in their environments. Yet ecology is by no means devoid of abstraction. To produce general principles out of the mass of complicated natural histories, ecology is replete with concepts, such as competition, evolution, and succession, and abstruse structures, such as communities and ecosystems.

The diversity of organisms and ecological concepts has always threatened to bury ecologists in a profusion of special cases. However, the notion of scale offers a framework for ordering nature that may help reveal generalities from the mass of particulars. Whereas the idea of scale is intuitively familiar to ecologists, the vagueness of intuition has contributed to ambiguity in defining and understanding the concept. Although formal ecological treatment of scale has been initiated in a collection of ideas called hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986, Pattee 1973), varying uses of scale remain in the ecological literature (see Carlile et

Various concepts associate with particular types of organisms in ecological research

al. 1989, Golley 1989, Meentemeyer and Box 1987, Milne in press).

In this article *scale* is defined by the temporal and spatial characteristics of energy and matter within and among ecological systems. The scale of a study is determined by the size and extent of the observations in time and space, as well as the resolving power of the individual measurements (Allen et al. 1984). We also subscribe to the premise that scale is defined by the observer. Scale may be defined as large or small only in relation to some reference—a benchmark that is often the scale of human observers and their primary experiences.

Despite emerging principles of scale, an ecologist's choice of scale for a study is often implicit in the selection of the study organism or ecological concept. It was our supposition that the often unrecognized relationship between organism/concept and scale should determine that some organisms pair with certain ecological concepts. We investigated the ecological literature to discover whether concepts and organisms were indeed paired. With this retrospective examination, we hope to raise ecologists'

awareness of scale-dependent relationships among organisms and ecological concepts and the implications of these relationships. The tangibility and familiarity of the organisms the ecologist counts or manipulates can lead to a false sense of objectivity. Considering scale in an explicit manner should result in measured judgment instead of the happenstance of unwitting choice.

Identifying the human scale in the ecological literature

We conducted a computer-assisted literature search on words found either in a title or in an author's list of keywords. A total of 23 taxa and 12 ecological concepts were used as keywords for the search (Table 1). Some of the taxa overlap or subsume each other, coming as they do from various levels at and above the family level. For example, both conifers and gymnosperms were used, the former being an important group defining a biome, whereas the latter is a taxonomic distinction equivalent to flowering plants or fern allies (these two plant groups were also targeted). Some taxa that were searched separately were aggregated for the analysis, such as families consisting primarily of trees. Any given reference could be entered under several keywords and so could be represented in the data more than once.

The computer searched *Biosis Previews*, a database of citations that draws on almost 9000 primary biology journals, symposia, reviews, preliminary reports, semipopular journals, se-

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lected institutional and government reports, and research communications. The search covered the period January 1969 to November 1984.

In the raw matrix, containing almost 339,000 references, some taxa were associated with many more papers than others. The keyword *mammal*, for example, retrieved more than 127,000 citations, whereas *bryophyta* retrieved less than 2000 citations. No taxon or concept scored so few citations as to be excluded from the analysis; island biogeography was the rarest category, with only 470 citations.

This study did not ask which organisms were studied most; therefore, the number of citations was standardized first by taxon row and then by concept column to yield a standardized measure of effort devoted to each pair of taxon and ecological concept. The data in the standardized matrix were inspected for the largest deviations from that expected from a random pairing of organism and concept. Deviation from expectation was defined as the difference between the observed (literature search) and expected (random pairing) research effort for each taxon/concept pair (Table 2). We identified potentially significant deviations by two criteria: deviations that exceeded ± 3 and deviations that were consistent in sign within a group of taxa or concepts. Groups were defined by inspecting the data matrix.

For the final analysis, the deviations matrix was transformed to binary form, with values above expectation being scored as 1 and values below expectation being scored as 0 (Table 3). The validity of our original supposition was examined by subjecting the binary matrix to principal component analysis, to depict graphically the relationships among concepts and taxa through simple ordination. This method of analysis is primarily used for data exploration and therefore associated with hypothesis generation, but failure to observe pattern in the principal component ordinations would certainly render our original supposition suspect and would indicate that further probing of detailed hypotheses would be unwarranted.

The primary assumptions for our interpretation were that the number of citations is a reflection of research

Table 1. The list of search keywords and abbreviations.

Organism taxa	Ecological concepts
Algae (ALGAE)	Disturbance (DIST)
Ascomycetes (ASCOM)	Succession (SUCC)
Basidiomycetes (BASID)	Evolution (EVOL)
Bryophyta (BRYO)	Community (COMM)
Pteridophyta (PTER)	Ecosystem (ECOS)
Gymnospermae (GYMN)	Island biogeography (ISBIO)
Coniferopida (CONIF)	Habitat (HABITAT)
Angiospermae (ANGIO)	Niche (NICHE)
Salicaceae*	Population (POPL)
Rosaceae (ROSA)	Resource capture (RESCAP)
Gramineae (GRAM)	Symbiosis (SYMB)
Betulaceae*	Competition (COMP)
Compositae (COMP)	
Fagaceae*	
Juglandaceae*	
Ericaceae (ERIC)	
Insects (INSECT)	
Fish (FISH)	
Amphibians (AMPH)	
Reptiles (REPT)	
Birds (BIRD)	
Mammals (MAMMAL)	
Lichens (LICHEN)	

*Indicates taxa that were aggregated as TREES for purposes of analysis.

effort; that the keywords reflect fundamentals of human perception of nature, rather than fashion in editorial policy (Abrahamson et al. 1989); and that our data transformation preserved taxon/concept relationships. We recognize that we may have missed some articles because they did not have the critical words in the strings that we searched. However, authors' decisions not to flag a concept or taxon is a reflection of their mind-set, which is part of what we wished to study. We also recognize that scientific disciplines define some key words uniquely or use different key words for the same concept. We did not investigate these different uses of key words.

Patterns in organism/concept relationships

From an examination of Table 2, it is immediately apparent that the deviations from expectation are subtle. No deviation is larger than the 15 over expectation scored by mammals for disturbance, and most deviations are less than ± 4 . This homogeneity is reassuring for the multivariate analyst and suggests that the results are not spurious artifacts deriving from the methods of analysis. If some of the deviations from expectations were large, then one might fear that the

matrix is an expression of only that one concept-taxon pair. Given the subtlety of the signal, any clear pattern that does emerge is likely to be reflective of a general trend across the entire discipline.

For many of the relationships there is little a priori basis for anticipating the outcome. However, some concept/taxon associations must satisfy classical biological relationships, otherwise the assumptions underlying the whole study are unsupported. If lichens are not the principal organism associated with symbiosis and that relationship is not secondarily reflected in the citations of algae and fungi (the taxa of the mutualism), then the entire study must be suspect. Table 2 does show one of the greatest positive deviations (13.20) from expectation to be between lichens and symbiosis.

Although it is not likely that the data set contains artifacts arising from arbitrary editorial policy, there is reason for concern that the results could be influenced by scientific fashion dictated by factors that have nothing to do with biology. One such factor could be founder effects in a given discipline where an organism, once picked, becomes the model of choice because of precedence. Fortunately, the data set appears homogeneous and the relationships have not

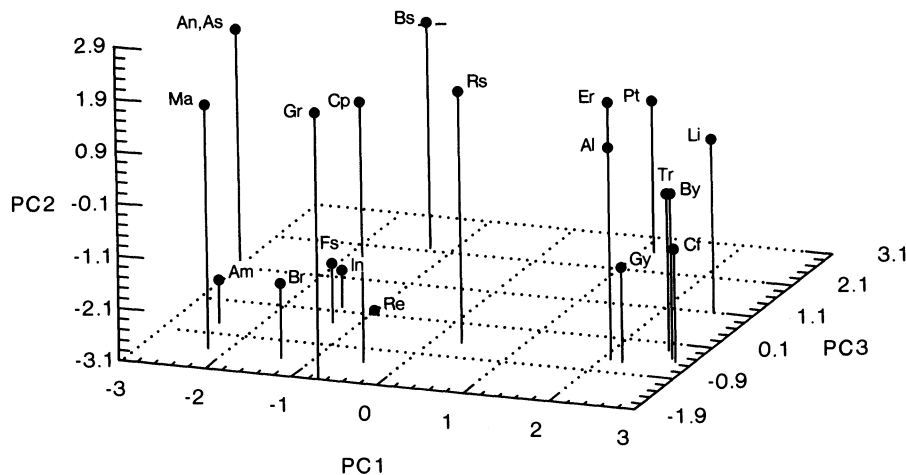


Figure 1. The first three principal components of the taxon ordination from the binary matrix (Table 3). The ordination of the quantitative deviations from expectation (Table 2) was similar, but the binary ordination gave more distinctive groups. Taxon names are abbreviated as in Table 3.

been dominated by any single-minded focus on a given concept using a particular taxon.

Plants versus animals. The principal difference observed in the literature was between plants and animals. All animals except mammals cluster tightly together away from plants in Figure 1. Although a multitude of factors are likely contributors, movement and physical size appear to offer a critical set of scaling factors that explain the pattern of separation.

Movement is an obvious scale difference between plants and animals. Although there are exceptions (e.g., consider corals versus dune-running

stoloniferous plants), what distinguishes plant from animal movement is the time scale of the movement. Compared with plants, animals (on average) occupy a larger area or volume in a shorter period of time. Because vagility is a fundamental attribute of organisms that underlies the concept of island biogeography, we should expect a disparity in research effort on this topic among plants and animals. The expected pattern is supported with significant (exceeding ± 3) negative deviations from expectation observed for the plant families *Ericaceae* and *Gramineae* and significant positive deviations for reptiles, birds, and insects (Table 2).

Although the majority of the plant taxa examined do not show strong negative deviations, the consistency in the deviation (10 out of 14 plant taxa) provides secondary evidence for the scaling difference between plants and animals based on mobility.

If we place birds on one extreme of the mobility continuum, then large plants would qualify as the other extreme. Movement in large plants is a low-frequency event because they grow slowly and move to a new site only after a long period of vegetative growth. Whereas movement is clearly an important scaling factor with large plants, an additional criterion is their physical size. There are few terrestrial organisms, other than large trees, that dwarf the human observer. Grieg-Smith (1971) noted that tropical forests are certainly diverse, but what is so impressive is the size of the organisms that display that diversity. As objects of study, forest plants appear suitably scaled for community work, particularly succession and ecosystem studies. There is a great block of these large plants and their associated epiphytes in the upper right corner of Table 3, all showing positive association with the concepts ecosystem, community, and succession.

Physical size also is an important scale criterion within plants. Small plants that are not associated with forests form a block in the middle left of Table 3 that scores above expectation for population-allied studies. This result suggests that a basic dis-

Table 2. The matrix of deviations from expectation for citations after standardization. Boldface indicates greatest deviation.

Taxon	COMP	DIST	POPL	SYMB	EVOL	RESCAP	ISBIO	NICHE	HABITAT	ECOS	COMM	SUCC
LICHEN	-4.14	-3.45	-4.31	13.20	-3.25	-6.13	2.89	-2.35	1.31	2.17	2.72	1.35
ALGAE	-2.67	-3.01	-1.38	7.51	-0.02	1.43	-2.68	-1.98	-2.95	3.80	1.71	2.67
ERIC	-1.25	1.04	-1.98	-3.07	-2.70	-2.65	-4.78	-0.41	1.86	1.86	5.69	6.39
TREES	-2.48	-0.88	1.92	-2.18	-3.22	-2.56	-1.64	0.14	0.26	4.18	3.63	6.64
BRYO	-2.99	-1.33	-3.03	-2.32	-1.23	-3.78	1.56	-0.55	3.87	0.68	5.81	3.35
CONIF	-1.56	-0.85	-0.97	-2.30	-3.24	-0.40	0.66	1.03	0.00	4.29	0.65	2.67
GYMN	-1.65	-0.89	-1.12	-2.26	-2.43	-0.63	1.56	1.03	-0.08	3.99	0.50	2.41
PTER	-2.99	-1.82	-2.14	3.09	4.52	-4.55	-1.29	0.28	2.99	-1.62	1.53	1.97
BASID	2.39	-0.54	0.30	6.27	0.16	-1.64	-2.97	-0.27	1.35	-1.94	-3.29	0.18
ASCOM	7.48	2.26	1.46	2.80	1.64	-4.27	-2.02	-1.54	-1.46	-2.20	-3.27	-0.86
ROSA	1.71	-0.20	2.80	-2.26	-0.85	-1.16	-1.00	-1.40	0.00	-0.40	1.32	1.46
GRAM	2.96	1.05	2.30	-2.09	-0.56	-0.21	-3.24	-0.84	-1.23	1.25	0.72	-0.12
COMP	0.78	1.28	0.32	-3.42	-0.17	0.74	-0.20	-0.47	0.09	-1.75	1.81	1.02
ANGIO	2.53	1.50	2.27	0.58	0.40	-0.95	-2.26	-1.04	-0.87	-0.28	-0.72	-1.20
MAMMAL	2.79	15.52	3.29	-1.21	-0.24	-3.10	-2.53	-2.68	-3.31	-3.08	-1.75	-3.67
FISH	-0.65	-2.25	1.48	-1.98	0.63	8.48	-0.75	1.00	-1.17	1.40	-2.10	-4.09
INSECT	-0.94	2.44	3.28	0.04	-0.30	3.19	3.65	1.68	-0.77	-1.06	-2.75	-3.62
BIRD	0.34	-0.75	0.95	-3.67	-0.34	2.51	6.22	3.68	1.38	-2.89	-3.37	-4.04
AMPH	2.38	-0.14	0.44	-2.45	6.71	2.68	1.36	0.63	-0.40	-3.38	-3.61	-4.15
REPT	-2.00	-4.10	-2.02	-4.27	4.49	13.00	7.87	4.08	-0.86	-5.02	-5.21	-5.95

Table 3. A binary translation of the matrix in Table 2. Citation occurrences above expectations were scored as 1, and citations occurrences below expectation were scored as zero. Abbreviations in parentheses are used in Figure 1 (rows) and Figure 2 (columns).

Taxon	COMP (Cp)	DIST (Ds)	POPL (Po)	SYMB (Sy)	EVOL (Ev)	RESCAP (Rc)	ISBIO (Is)	NICHE (Ni)	HABITAT (Ha)	ECOS (Ec)	COMM (Cm)	SUCC (Su)
LICHEN (Li)	0	0	0	1	0	0	1	0	1	1	1	1
ALGAE (Al)	0	0	0	1	0	1	0	0	0	1	1	1
ERIC (Er)	0	1	0	0	0	0	0	0	1	1	1	1
TREES (Tr)	0	0	1	0	0	0	0	1	1	1	1	1
BRYO (By)	0	0	0	0	0	0	1	0	1	1	1	1
CONIF (Cf)	0	0	0	0	0	0	1	1	1	1	1	1
GYMN (Gy)	0	0	0	0	0	0	1	1	0	1	1	1
PTER (Pt)	0	0	0	1	1	0	0	1	1	0	1	1
BASID (Bs)	1	0	1	1	1	0	0	0	1	0	0	1
ASCOM (As)	1	1	1	1	1	0	0	0	0	0	0	0
ROSA (Rs)	1	0	1	0	0	0	0	0	1	0	1	1
GRAM (Gr)	1	1	1	0	0	0	0	0	0	1	1	0
COMP (Cp)	1	1	1	0	0	1	0	0	1	0	1	1
ANGIO (An)	1	1	1	1	1	0	0	0	0	0	0	0
MAMMAL (Ma)	1	1	1	0	0	0	0	0	0	0	0	0
FISH (Fs)	0	0	1	0	1	1	0	1	0	1	0	0
INSECT (In)	0	1	1	1	0	1	1	1	0	0	0	0
BIRD (Br)	1	0	1	0	0	1	1	1	1	0	0	0
AMPH (Am)	1	0	1	0	1	1	1	1	0	0	0	0
REPT (Re)	0	0	0	0	1	1	1	1	0	0	0	0

inction exists between population and community concepts. The smallness of plants used in population studies allows those populations to be easily manipulated in an experimental setting. A characteristic of organisms used for population studies is that they are tangible to the investigator. Communities, on the other hand, are frequently studied with organisms that are too large for any species-specific collection to be tangible. Perhaps communities are intangible in some fundamental way.

Communities. Communities are composed of individual organisms integrated to such an extent that the processes holding the parts of the community together cannot be readily isolated. Therefore, communities do not appear to be composed of populations in any simple fashion. The community is the constraint put on population processes, not the aggregation of them, for it is the unexpected survival populations thought to be competitively inferior that give the community a special richness of pattern.

Different species occupy and interact with the landscape at different temporal and spatial scales, and in the community they accommodate each other in various interactions. If the community does not involve accommodation, then community is a bankrupt notion. Rather, accommodations

between species appear to be a significant part of nature.

Conceptually, the notion of scale and community ecology can be related through analogy to periodic phenomena. We can think of community members as having their own wavelength of longevity, reproduction, and period of movement or a returning pattern of occupancy on the landscape (Allen and Hoekstra 1989).

The relationships among different species involve periods of interaction, as well as periods in which species fail to interact with each other (Schoener 1982, Wiens 1977). This on-again, off-again series of exchanges gives a resonance among different organism wavelengths. Patterns of organisms on the landscape arise when the respective periods are close, but not identical. Although the relationship among the species coming together by happenstance might start as mere resonance, evolution presumably modifies the wavelengths or scales of the organism's life history in response to environmental constraints.

The accommodation between species and environment results in a true interference pattern. The interference involves both time and space, so, in general, one cannot think of the community as being in a particular place. In this conceptualization, the community is the accommodation itself, not necessarily the collection of species at

a place on the landscape. Therefore, it is intangible.

Whereas the physics metaphor and its focus on interactions offers one view of the community concept, an alternative conceptualization defines communities on the basis of species assemblages within definitive geographical and temporal boundaries. This dichotomy notwithstanding, plants have dominated the community ecology literature (Table 3). Communities are complex entities, and sessility of organisms simplifies their study. Vagile organisms are inherently difficult to observe, which makes study of their interactions difficult and identification of the assemblage's spatial and temporal extent enigmatic. With sessile organisms, one has the opportunity to observe directly species assemblages at scales consistent with human perception (small plants), or, as in the case of larger plants, at scales that have been made consistent with human perceptions through analysis (e.g., gradient analysis) or sampling (e.g., remote sensing).

Although both large and small plants appear to be used disproportionately for community studies, the interpretation of the community concept is not necessarily invariant to physical size of the organism. McIntosh (1973) asserts that the difference between F. E. Clements' (1905) holistic view and H. A. Gleason's (1926)

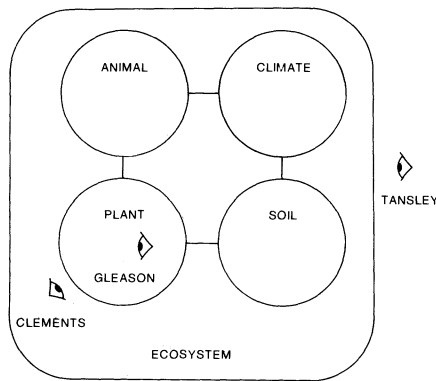


Figure 2. A schematic representation of the different scales of perception involved in the individualistic concept of community (Gleason 1926), viewed from inside the community, where the focus is on the autonomy of the component species; the superorganismal concept of community (Clements 1905), viewed from outside the community so as to emphasize its integrity; and Tansley's conception (1935) of the ecosystem, viewing the system from a greater distance, so that the autonomy of the biota is obscured as it is integrated with the physical environment. The three images of an eye represent the locations of the observer.

component view of community is that Clements dealt almost exclusively with prairie in Nebraska, whereas Gleason worked in the forests at the edge of the prairie in Illinois. Clements viewed the community as a highly integrated and discrete superorganism, whereas Gleason saw the community as being composed of species with varying tolerances and responses to environmental factors, resulting in a continuum of species composition.

Figure 2 shows how Gleason's individualistic concept of community is scaled so that the observer is inside the system, able to see the parts of the biota as separate. Being inside the system, the Gleasonian observer has difficulty seeing the whole and its emergent properties. Clements' superorganismal community emphasizes the integration of the whole, and so the observer is functionally outside the community system. From this larger-scaled perspective, a Clementsian is likely to lose a clear view of the independence of the parts of the biota. Superficially, the two views appear in conflict, but the contradictions may be more a matter of scale perspective than real.

Populations. Populations, by way of counterpoint to communities, have members of all the same species, and so each member occupies the landscape at a similar scale. Different life stages of a species population may vary in the scale with which they occupy the landscape, but within a life stage the organisms occur at the same scale. Therefore, there is no interference pattern. It follows that being a collection linked by behavior or genetics or both, the population can be considered as occupying a place on the landscape at any instant in time. It may move or disintegrate, but at one instant the population has a place and therefore is a tangible on the ground. Accordingly, organisms that are scaled relative to ourselves such that we can see the collection of individuals and their dynamics in a place are favored for studies of population phenomena. Small plants and animals are strong candidates for this role (Table 3).

Although both small plants and animals exceeded expected population research, only animals (insects and mammals) scored above our arbitrarily selected significance level (± 3). One problem with the use of plants, lichens, and bryophytes in population studies is the difficulty identifying individual organisms.

Competition. The contrast between communities and populations can be further highlighted by comparing the role of competition in the two concepts. Interspecific competition has, in the recent past, been considered of primary importance in explaining patterns in community structure (Murray 1986, Roughgarden 1983, Schoener 1982, Strong et al. 1984). However, elevation of the competition concept to a universal principle of community organization was premature. Competition within communities can be so recursive that it is indistinguishable in the web of interactions from such factors as environmental heterogeneity, mutualism, and commensalism. Competition is not allowed to equilibrate into competitive exclusion, a characteristic of the interactions of unrestrained populations.

In a community, the populations interdigitate so finely that they cannot be seen to have integrity. Accordingly,

interspecies population-competition is not to be expected as the sole explanatory principle for communities and may in fact only be relevant under a limited set of conditions (Connell 1983, Schoener 1982). Neighborhood competition, the competition of paired individuals, might be relevant in simple communities, but generally the paired interactions become obscured long before the scale of the community is achieved.

These relationships among competition, communities, and populations are consistent with the separation of competition and population from community in the ordination of concepts (Figure 3). The organisms that are used disproportionately often for population and competition studies are not generally trees, but taxa with large representations of herbaceous plants (Table 3).

These same taxa are also used often for disturbance studies. The explanation for these patterns in the data is again organism size. Small plants in large numbers can be surveyed by observers on the ground, and mosaics of populations of different species are commonly apparent. Disturbance scars can be seen easily. Furthermore, growth processes are faster in herbaceous plants, so the disturbance scars can be seen to heal in real time. Also, herbaceous plants can be observed to jockey for position during a short period. With herbaceous plants, we can observe entire populations, their competitive dynamics, and their response to disturbance. Competition is exactly the right sort of small-scale, fast dynamic to be an explanatory principle for the outcome of population interaction of fast-growing herbaceous plants. It does not matter that some trees grow faster than some herbaceous plants, for the consideration is not absolute quantity, but is change as judged significant by the human observer. A tree must grow a lot before the observer notices that the species dominance is shifting.

Evolution. Much in the manner that communities are too large to yield to fine-grained explanations like competition, evolution is also likely to require coarse-grained explanations. Conventionally, evolution is viewed as the consequence of populations in competition. Obversely, competition

has been described as having both ecological and evolutionary consequences (Abrams 1990). If this is indeed the case, then organisms that are represented in population and competition studies with greater regularity than expected may also receive disproportionate use for evolutionary studies.

Our results do not support the idea that studies of competition between populations contribute to understanding evolution. Many organisms apparently well suited to studies of competition do not emerge among those used in an abundance of evolutionary studies (Table 2). In the ordination of concepts (Figure 3), evolution is nowhere near the population-competition-disturbance concepts. Taxa emerging as favorites for evolutionary studies are at first a strange mixture: reptiles, amphibians, and pteridophytes. However, they are all ancient orders. The long lineage appears to be the critical scaling feature of evolution.

Ecosystems. Organisms are not usually identifiable as entities in the concept of ecosystems. Rather, they are part of pathways that may involve only parts of the organism (e.g., tree roots) or guilds (e.g., mycorrhizae). The functional ecosystem is a black box, which is reflected in the very strategy of input/output modeling. In terms of observation scale, the observer is operationally outside the system and thus the organisms are not apparent, even though the biota are an important part of the system.

Given this property of the ecosystem concept of nature, taxa that live in habitats where the ecological observer cannot see them are likely candidates for ecosystem studies. Animals are consistently negatively associated with the ecosystems (Table 3), with the exception of fish. This exception highlights the nature of ecosystems and their relationship with the human observer and is expected if the taxon represents a functional ecosystem compartment, as fish do for secondary consumption and nutrient storage. Similarly, algae are unseen (as individuals or species) primary-production and nutrient-capture compartments, explaining their high score in the ecosystem column. In the ecosystem, the biota do not

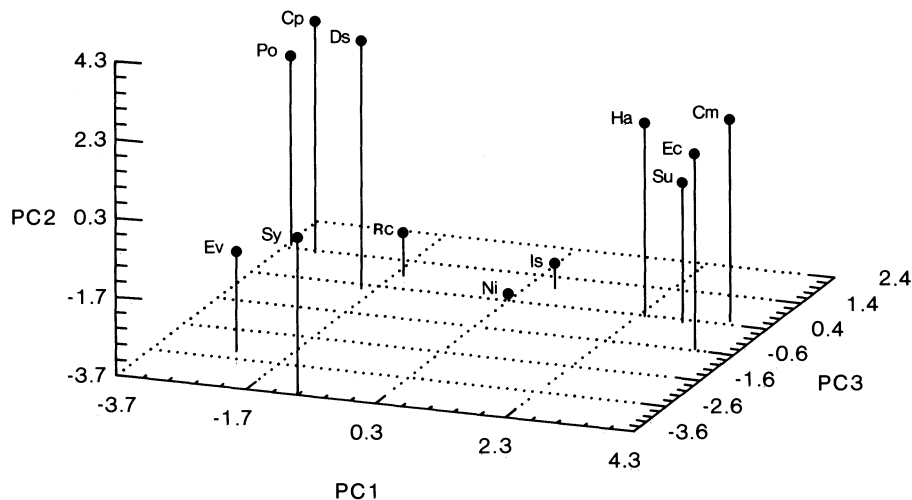


Figure 3. The first three principal components of the concept ordination from the binary matrix (Table 3). The ordination of the quantitative deviations from expectation (Table 2) was similar, but the binary ordination gives more distinctive groups. Concept names are abbreviated as in Table 3.

have to be seen as separate individuals or taxa, but rather they are integrated with the physical environment through process (O'Neill et al. 1986).

The ecosystem view of Tansley (1935), where the observer is outside of a system that integrates the biota and its physical environment, appears to involve a more coarse view of the world than used by community ecologists (Figure 2). Note that grasses, as the undefined species of primary production for grazers, occur in ecosystem studies, whereas Compositae in their petaloid splendor do not. Because of their taxonomic intransigence (one needs a hand lens to key them out), grasses are naturals for a role in a conception of nature that calls all green material one thing—primary production.

Analysis summary. The unique scale of the observer in relation to the taxon and ecological concepts studied is elucidated by the analysis results. In both the ordinations of concepts and taxa, the clusters are too tight and are too easily explained to be spurious depictions of how ecology has been studied. High on the second component axis of the concept ordination (Figure 3) are two well-defined clusters, at opposite ends of the first component axis. The positive association of the small plants with competition, population, and disturbance yields the tight cluster on the left; the forest taxa are responsible for the distinct

group of habitat, community, succession, and ecosystem in the upper right. This latter group also gains cohesion by a strong negative association with animals. The ordination of taxa (Figure 1) similarly gives three distinct groups, each with its easily interpretable, distinctive scale characteristics: big forest plants and their associates, small plants, and animals.

The analysis we present has been biased by our backgrounds. Others with different frames of reference will undoubtedly have suggestions for additional taxon/concept keywords and will observe different patterns and pairings. For example, animal ecologists might note that niche and island biogeography concepts seem to have a close association in Figure 3. Also evolution and symbiosis show potential for a conceptual relationship.

Neither of these pairings met our criteria for significant deviation from expectation, but they point toward opportunities for further study. The merit of this type of analysis, therefore, is not just in its depiction of how ecological research has been conducted, but, more important, in its heuristic tendency to encourage further investigation among an eclectic group to uncover scale-dependant relationships.

Conclusions

As a preliminary to any ecological study, ecologists organize their

thoughts around a set of tangibles, many of which are organisms. However, the scaling of organisms is far from simple. Scales intrinsic to the organism include: size, the time periods associated with reproduction, longevity, and rates of movement. Beyond this simple group are extrinsic factors: scaling relative to other organisms, scaling relative to the physical environment, and scaling relative to patterns of human perception. To deal with the interactions of these differently scaled organisms, the ecologist employs various abstractions that also have an implicit scale relative to the organism. Some of these scales mesh more easily than others, and so various concepts associate with particular types of organisms in ecological research. Sometimes an insistence on some particular type of explanation forces incompatible scales together.

In this article, we have used the patterns of success in the past, manifested in the broad patterns in published research, to describe the matching of the study site and organisms with concepts. From this investigation, it emerges that the mobility of animals makes them difficult conceptual bedfellows with plants. Botanists have reason for their world view being at odds with that of the zoologists. Rather more surprising, herbs apparently cannot be readily studied alongside larger plants, because the difference in scale means that it is difficult to find a set of unifying concepts that apply in the same way to such a heterogeneous set of organisms.

Despite their best efforts to achieve objectivity, ecologists use a remarkably provincial set of relative scales. Big and small, fast and slow, and near and far are scaled relative to human size, longevity, mobility, and acuity. Ecologists say that a bird moves far because they cannot see it when it has

finished moving. It moves fast because it gets to its destination before the human observer could. Because science hopes to enhance understanding, necessarily in human terms, it may not be bad that ecology is scaled in human terms. Rather than fight human nature, ecologists are well advised to be explicit about the scales they use, so that they can anticipate the consequences of decisions that were formerly made subconsciously. By modeling with appropriately scaled concepts, ecologists can hope to advance with fewer delusions of objectivity, but more consensus. By recognizing the importance of relative scaling inside concepts as well as in the scale of tangibles, ecologists can hope to match best the questions to the study site, compatible concepts, and data.

We are not reporting ecology the way it should be studied, but rather the prevalent way it is studied. Ecologists who find themselves focusing on an area that received less than expected attention might take note of the fact that they are taking an unorthodox stance, and thereby they might be able to step beyond conventional wisdom.

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