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VARIATION IN SPECIES RICHNESS: TOWARDS A UNIFICATION OF HYPOTHESES

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Abstract: The question, "why do areas vary in species richness?" has been important throughout the history of ecology. It is difficult to answer definitively because we have so many (at least 120) plausible hypotheses. This abundance of hypotheses has led to a number of attempts to classify them. Unfortunately, richness hypotheses often defy such categorization. Instead of placing species richness hypotheses into categories, I suggest an alternative approach: to treat species richness hypotheses as violations of the assumptions of Gause's Competitive Exclusion Principle. This is a very similar approach to the pedagogy of population genetics: evolution occurs if and only if at least one assumption of the Hardy-Weinberg principle is violated. The classification of hypotheses advocated here treats interspecific competition as a central organizing concept in community theory. However, it does not treat competition as an organizing concept in **communities**: indeed, the relaxation or disruption of competition is considered to be the status quo in the majority of communities.

INTRODUCTION

MACARTHUR's (1965) seminal paper on diversity begins with the simple sentence, "Patterns of species diversity exist". Ecologists have attempted to understand why communities vary in the number of coexisting species ever since ecology became a self-conscious discipline almost a century ago (MCINTOSH 1985, KINGSLAND 1991). It is both impressive and humbling that a symposium on coexistence is needed in 1992.

The problem at hand is answering the question "why do so many species coexist?" or almost equivalently, "what causes variation in species richness?" We cannot dismiss such questions by saying variation in richness is random, because in the majority of cases it clearly is not. Direct tests of variation in species richness often demonstrate substantial deviations from randomness (PALMER 1987, 1990, WILSON et al. 1987). More importantly, as is pointed out by numerous ecology textbooks (e.g. RICKLEFS 1979, BEGON et al. 1990, SMITH 1990), species richness is predictably related to important environmental gradients, such as altitude (TERBORGH 1977), area (GLEASON 1925), biomass (GRIME 1973), body size (MAY 1988), depth for aquatic organisms (REX 1981), disturbance (CONNELL 1978), fertilization (SILVERTOWN 1980), habitat diversity (HARMAN 1972), island characteristics (MACARTHUR & WILSON 1967), latitude (CONNELL & ORIAS 1964), soil pH or cations (PEET & CHRISTENSEN 1980), precipitation (BROWN & DAVIDSON 1977), predation (LUBCHENCO 1978), successional time (AUCLAIR & GOFF 1971), and zonation along lake shores (NILSSON & WILSON 1991). As PIANKA (1966) pointed out, "... any species diversity gradient might be a suitable study system" for exploring variation in the degree of coexistence.

SPECIES RICHNESS HYPOTHESES

Throughout the history of science, unexplained scientific phenomena have been accompanied by a small set of plausible hypotheses (BUTTERFIELD 1957). Indeed, most ecological phenomena fit this mold; it is rare to find an ecological paper which cites more than half a dozen hypotheses to account for the patterns observed. The science of coexistence is an exception. Attempts to explain coexistence, variation in species richness, and/or diversity gradients have resulted in a proliferation of hypotheses. Tab. 1 (see Appendix) lists 120 hypotheses which have been proposed to account for variation in species richness. Despite the length of the list, it is merely the result of a cursory overview of the literature. An exhaustive investigation would undoubtedly yield a much longer list. The number of hypotheses to explain richness patterns is so overwhelming that some authors (e.g. PAGEL et al. 1991) are almost apologetic about introducing new ones.

It must be admitted that many of the listed hypotheses are synonyms or near-synonyms. For example, the spatial mass effect and the seed reimmigration concept are synonyms (although the latter is clearly only relevant for higher plants). Also, habitat diversity, environmental heterogeneity, and spatial variability are essentially equivalent. Some hypotheses are special cases of other hypotheses; e.g. the niche dimensions hypothesis can be considered (under certain circumstances) a special case of the environmental heterogeneity hypothesis. Some hypotheses are only relevant for particular systems; the Keystone Granivory Hypothesis obviously does not pertain to snails grazing on algae. Hypotheses predicting the diversity of phytophagous insects in relation to plant chemistry (e.g. those proposed by JONES & LAWTON 1991) can be considered special cases of other hypotheses. However, lumping hypotheses together can be semantically difficult. For example, while many authors treat "habitat heterogeneity" as synonymous with "habitat diversity", NILSSON et al. (1988) argue that the two are distinctly different. Even if the same name is used, different authors often have subtly different interpretations of a hypothesis.

Classification of hypotheses

Even after combining synonyms and removing special cases, Tab. 1 (see Appendix) remains a formidable list. If the philosopher of science POPPER (1935) was correct in stating that science only progresses through the falsification of hypotheses, we must sadly conclude that the study of coexistence has not progressed far. The majority of hypotheses seem quite plausible for at least a limited set of conditions. It is unlikely that many of them can be completely and universally falsified.

A number of authors have attempted to solve the apparent dilemma of an overabundance of hypotheses by categorizing hypotheses in various ways (Tab. 2). Repeated classifications may appear to be wasted effort, yet each of the treatments listed in Tab. 2 offer distinctly different (yet largely complementary) ways of looking at the same phenomena, hence enriching our understanding of coexistence.

Nevertheless, there are inherent drawbacks to such classification schemes. This is because many hypotheses do not fit neatly into categories, as is evidenced by subtle (and not so subtle) discrepancies in past attempts. Examples of this lack of fit are given below.

Table 2. Classifications of hypotheses explaining variation in species richness, along with key features of the classification.

AARSSEN (1992)	Influence of genetics on coexistence, and vice versa
AUERBACH & SHMIDA (1987)	Spatial scale of operation
BROWN (1988)	Good review for animals
CONNELL (1978)	First review to distinguish equilibrium and nonequilibrium hypotheses
CONNELL & ORIAS (1966)	Relates hypotheses to energy flow and stability
DIAMOND (1988)	The "QQID" approach: resource Quality, Quantity, Interactions, and Dynamics
GILLER (1984)	Each hypothesis is related to species saturation, niche width, and resource diversity in a manner true to MACARTHUR (1965).
WILSON (1990)	Good "synonymy" of hypotheses. This is also the only review I am aware of which relates hypotheses to patterns observed in a given region.

Other classifiers and listers of hypotheses include HUTCHINSON (1959), SIMPSON (1964), PIANKA (1966), SANDERS (1968), PONTIN (1982), CRAWLEY (1986), BENGTSSON et al. (1994), and numerous textbooks.

Classification problems with the resource ratio hypothesis

TILMAN'S (1982, 1985) resource ratio hypothesis predicts that more species coexist at low levels of resources because the plants **perceive** the environment as inherently more spatially variable than they do at high resource levels. Thus, paradoxically, the environmental variability hypothesis can operate even if regions do not vary in the magnitude of environmental variability. The resource ratio hypothesis is an equilibrium hypothesis, since it assumes that resource use is in equilibrium with resource supply. Nevertheless, the model attempts to explain successional change in two very different ways, without divorcing itself from its equilibrium foundation: (a) redefining disturbance as the supply rate of open space allows us to predict equilibrium coexistence at spatial scales much larger than the disturbed patch (TILMAN 1982, Ch. 8), and (b) by assuming that resource levels change at a much slower rate than species equilibrate with these resources, species are in equilibrium with a "successional trajectory" within a patch (Ch. 9). Apparently, the resource ratio hypothesis ignores situations between these two extremes. Nevertheless, the different uses of the resource ratio hypothesis with respect to disturbance make it impossible to classify.

Classification problems with the intermediate disturbance hypothesis

The intermediate disturbance hypothesis (IDH) (CONNELL 1978, HUSTON 1979, 1985, PETRAITIS et al. 1989) predicts highest diversity at intermediate "levels" of disturbance, where the "level" can refer to the intensity, frequency, size, or time since disturbance. The IDH is hard to classify because it is actually a set of different interconnected hypotheses which potentially fit into many categories.

The IDH predicts high richness at intermediate times following disturbance. The reasoning behind this is that few colonizing species are present at early stages of succession, and competitive exclusion precludes many species coexisting late in succession. The high richness at intermediate times can be due to two (not necessarily conflicting) processes: high species overlap because early successional species persist in the presence of late successional species (temporal mass effect) and the fact that competitive exclusion has not yet had time to drive subordinate species to extinction (nonequilibrium coexistence).

Changing the disturbance regime may also have complex effects on the interpretation of the IDH (Fig. 1). Landscapes with infrequent disturbance consist mostly of old patches, and hence environmental heterogeneity is low. Landscapes with very frequent disturbance consist of only young patches, also generating very low heterogeneity. However, landscapes with intermediate frequency of disturbance will tend to have patches of many different ages, and hence many different environments. At the landscape scale, high richness at intermediate disturbance frequency can be caused by the environmental variability hypothesis. On the patch scale, highest richness is also expected at intermediate disturbance frequency. This is because patches at intermediate frequency are more likely to be surrounded by patches with different characteristics. Hence, the spatial mass effect will be strongest in landscapes with intermediate frequency disturbance.

Intermediate **intensity** of disturbance can also promote high richness in multiple ways. A moderately intense disturbance can enhance richness temporarily through nonequilibrium coexistence, whereas a severe disturbance would cause extinction. However, the environmental variability hypothesis may also be operating: For example, a forest with 50% of the trees uprooted by windstorm will have a much wider array of microhabitats available, and hence higher richness, than comparable forests with near 0% or near 100% of the trees uprooted. COLLINS (1992) segregates this kind of phenomenon from the IDH and considers it the "disturbance heterogeneity model".

Categorization problems due to conceptual problems

A number of hypotheses are hard to classify because they depend on ecological concepts which are open to various interpretations. For example, many hypotheses (e.g. fundamental niche differentiation, habitat differentiation, habitat diversity hypothesis, niche breadth, niche dimensions, niche diversification, niche overlap, etc.) depend on varying concepts of niche and habitat. If we follow ODUM's (1959) distinction of the habitat as an organism's **address** and the niche as the organism's **profession**, then plants and other sedentary organisms don't fit easily into these categories. What plants **do** is so inseparable from where they **are**, that niche differentiation and habitat specificity are practically synonymous. WHITTAKER et al.'s (1973) distinctions between niche, habitat, and ecotope are promising, but still rely on an ambiguous definition of community. Perhaps the only distinction that can be made, albeit arbitrarily, is that niche differentiation occurs within sites, and habitat specificity occurs among sites, with the spatial bounds of a "site" being left up to the observer.

Other classification problems

Categorization of hypotheses might also be difficult because changing spatial scale can cause the same phenomenon to be explained by different hypotheses. For example, species can coexist temporarily within a disturbed patch (i.e. nonequilibrium coexistence). However, species can coexist permanently on the scale of many patches if there is a constant disturbance regime. This constitutes a prime example of niche or habitat differentiation if disturbed conditions are viewed as a resource for some species but not others.

Hypotheses have also been classified according to whether the mechanisms operate on evolutionary or ecological time (ZOBEL 1992). However, evolutionary change can occur in

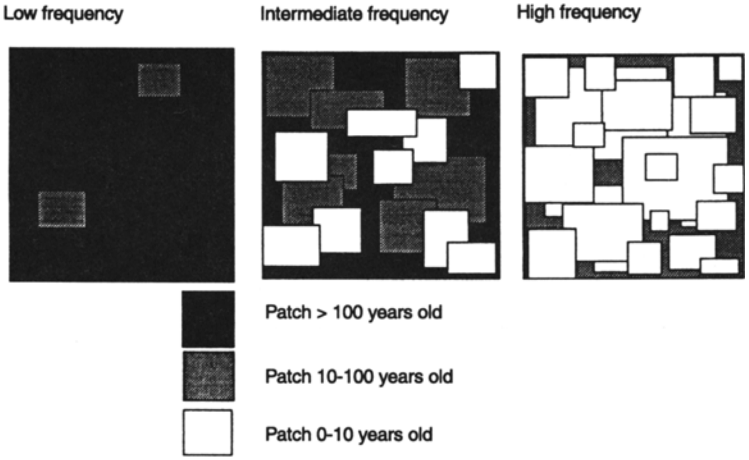

Fig. 1. Three hypothetical landscapes with constant disturbance regimes of varying disturbance frequency.

time periods short enough to be considered "ecological". The distinction between origin of species richness and maintenance of species richness (Janzen 1970, Brown 1988) is likewise arbitrary: taxa must be maintained in the community and/or landscape throughout the speciation process. Also, the "origin" of species on islands or habitat islands is from an external "species pool" - but this pool cannot exist indefinitely unless it is maintained.

Another commonly made distinction between determinants of richness is whether processes are local or regional (Ricklefs 1987, Cornell & Lawton 1992). This approach does not appreciate the fractal nature of landscapes (Burrough 1981, Palmer 1988, 1992, Milne 1991, Williamson & Lawton 1990), which implies that there is a continuum between "localness" and "regionalness". Since richness gradients exist over a wide range of spatial scales (see Palmer 1990b), explanations must be targeted at a wide range of scales, without assuming any scales to be "local" or "regional". No matter what the spatial scale, a duality exists: richness is determined by processes both inside and outside the community.

The difficulty in classifying richness hypotheses has been recognized for some time. Sanders (1968) recognizes the ambiguity in Pianka's (1966) treatment by stating "most of the hypotheses contain elements of more than one grouping". Indeed, Pianka admitted the ambiguities in the initial paper. Brown (1988) suggested that different hypotheses are not strictly comparable because they aim at different levels of explanation.

To summarize, hypotheses explaining variation in richness do not always fit neatly into categories, and synonymy among hypotheses is not always straightforward to decipher. It may be impossible to produce a classification scheme without ambiguities; indeed, according to Gödel's theorem it is fundamentally impossible to create any formal classification which is simultaneously complete and correct (Hofstadter 1980). I suggest a method to deal with the plethora of hypotheses which is fundamentally different, and that is to parallel one of the most successful paradigms of population genetics, that of the Hardy-Weinberg equilibrium.

Table 3. The Hardy-Weinberg Principle of Genetic Equilibrium (Hardy 1908); this version is modified after Jenkins (1979).

The Principle:

Given a population of sexually reproducing organisms, the proportions of alleles, genotypes, and phenotypes will not change through time. That is, evolution will not occur.

Conditions of the Principle:

(1) The population size is infinite
(2) There is no net mutation of alleles
(3) Mating is random (i.e. there is no sexual selection)
(4) All genotypes (and hence phenotypes) must be equally viable, fertile, and fecund (i.e. there is no natural selection)
(5) The gametes must be equally capable of forming zygotes (i.e. there is no meiotic drive or gamete selection)
(6) There is no immigration
(7) There is no emigration

Corollary:

The amount and/or rate of evolution is positively related to the degree to which the above conditions fail.

The Hardy-Weinberg Principle as a model

Population genetics attempts to explain how and why populations evolve (i.e., allele frequencies change). Ironically, geneticists place at the very center of their theory the Hardy-Weinberg Principle (HWP), which states that populations will tend **not** to evolve (Tab. 3). However, we know for a fact that populations do evolve. Thus, in any particular case of an evolving population, at least one of these conditions must be violated. For example, genetic drift will cause evolution if populations are finite [violation of condition (1)], and natural selection will cause evolution if there is differential reproduction and/or survival of phenotypes [violation of condition (4)]. Furthermore, the **amount** of evolution is related to the **degree** to which these conditions are violated. Very small populations are expected to have more pronounced genetic drift than large (but finite) populations, and strong selection pressure will result in a more rapid change in allele frequency than will weak selection pressure.

This simple formulation of evolution has allowed geneticists to separate the relative importance of different evolutionary forces, as well as to examine their interactions. It has done this in a way a simple categorization of hypotheses could not.

I propose that community ecologists treat coexistence in an analogous way: mixtures of species will tend toward monocultures if and only if the conditions of the Competitive Exclusion Principle hold.

The Competitive Exclusion Principle

The Competitive Exclusion Principle (CEP) has been a part of ecology for over a century, but it was Gause (1937) who placed the principle as a central organizing concept in community ecology (Kingsland 1991). Over the years, the principle has been given a variety of names and a variety of definitions, depending on the perspectives of the authors, and the terminology and ideas in vogue at the time (Tab. 4). However, all definitions are consistent in stating that competition will prevent indefinite coexistence unless species differ.

Tab. 5 presents the reformulation of the CEP after the HWP model. It begins with the statement that competition will result in complete dominance of one species, but then is followed by a number of conditions. Since we know that species coexist, and that frequently many species coexist, we know that the conditions must be violated in nature. Most of the hypotheses listed in Tab. 1 can be considered cases where the conditions in Tab. 5 are broken or modified, as indicated by the superscripts. Since as previously explained, authors interpret the same hypotheses in subtly different ways, I expect some disagreement with the superscripts.

The idea behind Tab. 5 is not unique to this paper. HUTCHINSON (1957) stated that the CEP "... is true except in cases where there are good reasons not to expect it to be true." CRAWLEY (1986) considers species rich systems to violations of the conditions of the CEP. However, neither Hutchinson nor Crawley formally circumscribe what the violations of the CEP are.

Violations of conditions of the CEP

Condition (1) states that time has been sufficient to allow exclusion. The concept of nonequilibrium coexistence is an example of the violation of this condition. A steady-state "climax" rarely occurs because disturbance and/or climatic variability is too rapid to allow complete competitive exclusion. The Niche Overlap Hypothesis implies that for some reason, species in species-rich communities are able to overlap more in their resource requirements than species in species-poor communities. This "reason" can be insufficient time for competitive exclusion. Communities which have not yet reached equilibrium will tend to have higher species richness than those which have.

Species can also coexist if the environment varies temporally [violating condition (2)], as predicted by the gradual climate change, spatiotemporal heterogeneity, temporal variability, and time partitioning hypotheses. Communities with high temporal variability will tend to have more species than temporally stable communities. Temporal heterogeneity can be allogenic (e.g. gradual climate change) or autogenic (e.g. shifting competitive hierarchy). Some explanations involving temporal variability (e.g. ecological time hypothesis, evolutionary time hypothesis, glacial extinction hypothesis) are not actually violations of condition (2), but rather with the premise of the CEP: for historical reasons, the initial suite of species varies in size.

Probably the most common reason for variation in richness is that condition (3) is violated. A spatially varying environment allows species with different requirements to coexist (environmental heterogeneity, habitat diversity, spatial variability). Having dissimilar environments in close proximity also allows the persistence of species which would normally be outcompeted (spatial mass effect, seed re-immigration concept). Spatial variation in the environment is such an obvious and incontrovertible cause for coexistence that observers often restrict their investigations to "apparently homogeneous" regions. Unfortunately, the environment in "apparently homogenous" regions is often quite variable at small spatial scales (cf. PALMER 1990a, LECHOWICZ & BELL 1991), and it may be **in principle** impossible to factor out the effects of environmental microheterogeneity in the field (PALMER & DIXON 1990).

Condition (4) is violated when species differ in their resource requirements to the degree that they are limited by different resources (resource ratio hypotheses, niche diversification

Table 4. Selected definitions of the Competitive Exclusion Principle (also known as Gause's Rule, Gause's Law, Gause's Hypothesis, Gause's Principle, Volterra-Gause Principle, Grinnell's Axiom, and Volterra-Lotka Law).

"It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships" (GRINNELL 1917)

"The steady state of a mixed population consisting of two species occupying an identical "ecological niche" will be the pure population of one of them, of the better adapted for the particular set of conditions" (GAUSE 1937)

"Two species with the same niche requirements cannot form steady state populations in the same region" (HUTCHINSON & DEEVEY 1949)

"multiple, sympatric occupation of a niche cannot long endure" (SIMPSON 1964)

"only one species population can have the same set of biological characteristics and responses to physical parameters, and so be associated with the one particular ecological niche, and vice versa" (BOUGHEY 1973)

"The elimination of one species by another as a result of interspecific competition" (ODUM 1975)

"Two or more species cannot coexist on a single resource that is scarce relative to the demand for it" (RICKLEFS 1976)

"Two species with the same ecology cannot coexist" (HARPER 1977)

"complete competitors cannot coexist indefinitely" (GILLER 1984)

"one niche, one species" (BARBOUR, BURK & PITTS 1987)

"Two species cannot occupy the same niche" (BREWER 1988)

"If two competing species coexist in a stable environment then they do so as a result of differentiation of their realized niches; but if there is no such differentiation, or if it is precluded by the habitat, then one competing species will eliminate or exclude the other" (BEGON et al. 1990).

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hypothesis). In Lotka-Volterra competition models (WILSON & BOSSERT 1971), this is equivalent to the competition coefficients being less than 1 (the impact of interspecific competition is less than that of intraspecific competition). Likewise, in de Wit replacement series models (HARPER 1977), condition (4) is violated when the relative yield total is greater than 1; i.e. when organisms in polyculture are more able to fully utilize resources than the same species in monoculture. This can be labeled the "Jack Spratt phenomenon" after the old nursery rhyme:

> Jack Spratt would eat no fat;
> His wife would eat no lean.
> And so, between the two of them,
> They kept the platter clean.

Species richness will tend to be high in regions in which species tend to be limited by different resources.

Violation of condition (5) is equivalent to stating that species richness is regulated. In general, a community with an advantage to rarity will have more species than a community with no such advantage (e.g. compensatory mortality hypothesis). A special case of violating condition (5) is when seedlings of species other than the canopy tree have a disproportionate advantage (e.g. Janzen-Connell, alternation of species, and reciprocal replacement hypotheses). Condition (5) can be violated in subtle ways. For example, indefinite coexistence is possible if the inferior competitor has high variation in individual growth rates (HARA 1993). It is likely that this is the dominant mechanism of coexistence in species-rich grasslands

Table 5. A reformulation of the Competitive Exclusion Principle.

The Principle:

Given a suite of species, interspecific competition will result in the exclusion of all but one species.

Conditions of the Principle:

(1) Time has been sufficient to allow exclusion
(2) The environment is temporally constant
(3) The environment has no spatial variation
(4) Growth is limited by one resource
(5) Rarer species are not disproportionately favored in terms of survivorship, reproduction, or growth
(6) Species have the opportunity to compete
(7) There is no immigration

Corollary:

The greater the degree to which these conditions are broken, the greater the number of species which can coexist.

which are regularly mowed, grazed, or burnt - but it remains to be demonstrated that the biomass of common or dominant species is disproportionately removed (i.e. the tall poppy hypothesis). Preliminary results from simulations by the author (unpubl.) indicate that the correlation between abundance and proportion of the biomass removed need not be particularly strong in order to guarantee the coexistence of a large number of species.

Condition (6) is violated if the geometry of the environment precludes competition. If new sites are made available stochastically, are spatially disjunct, and the first colonists will be the indefinite occupants, then high richness will be permitted due to lottery establishment. If a barrier exists between two virtually identical pieces of habitat, ecological equivalency will allow coexistence of **potential** competitors because the species are not permitted to be **actual** competitors. Communities with a large number of such barriers are likely to have more species coexisting than those with fewer barriers (LEVIN 1974).

Condition (7) is very similar to condition (6) of the HWP (Tab. 3). Species richness will be enhanced by continual immigration of new species, even if long-term coexistence is impossible. Communities with much immigration will tend to be richer in species than those without much immigration. Condition (7) is violated by hypotheses related to island biogeography theory and the mass effect.

Factors qualifying conditions of the CEP

A number of explanations brought forward to explain coexistence are not directly violations of the CEP, but are better described as modifiers of the conditions. Most of these involve condition (1) - and modify the **rate** of competitive exclusion. For example, HUSTON's (1979) version of the intermediate disturbance hypothesis describes how high richness is expected in unproductive regions because competitive exclusion is much slower than in more productive regions. HART (1990) and TAYLOR et al. (1990) speculate that elevated rates of competitive exclusion coupled with reduced species pools favor low diversity vegetation.

Increasing the similarity among species' resource requirements will tend to slow down exclusion [and hence modify condition (1)]; it takes a longer time for the competitively superior species to achieve dominance if it is almost evenly matched by other species. For example, long-term coexistence has been predicted in systems where different plant species are infected by the same mycorrhizal symbiont, thereby increasing similarity of nutrient requirements (JANOS 1983, CONNELL & LOWMAN 1989). AARSSEN (1983) speculates that natural selection might actually cause species to converge in resource requirements, hence delaying competitive exclusion. However, such a process is unlikely because models of population genetics (e.g. MILLIGAN 1985) predict that species will almost always **diverge** in requirements. In addition, genetic convergence in resource use has yet to be convincingly demonstrated in the field (LUESCHER & JACQUARD 1991).

Increasing the spatial scale of study will generally result in retarding dynamics (DEANGELIS & WATERHOUSE 1987) and hence in delaying competitive exclusion. Increasing spatial scale will also, on average, increase environmental heterogeneity. Thus hypotheses relating area to richness are potentially modifications of more than one condition of the CEP. The aggregation hypothesis also modifies more than one condition: ATKINSON & SHORROCKS (1981) demonstrate that aggregation within a species will tend to slow down competitive exclusion rates [condition (1)], and spatially aggregated species have less opportunity to compete than well-dispersed species [condition (6)].

Disturbance, predation, and Gause's Principle

Disturbance is commonly thought of as an event which prevents competitive exclusion. Then why is it not included in Tab. 5? This is because it can be considered to affect communities through the factors already listed. By continually resetting the successional clock, it can violate condition (1). It can create spatial and temporal variation, thus violating conditions (2) and (3). Even a fairly simple disturbance such as mowing affects common species disproportionately (GRIME et al. 1987) and hence violates condition (5). Disturbance may also create isolated "patches" which allow ecological equivalency or lottery competition to occur, violating condition (6). The reformulation of Gause's principle makes it clear that moderate disturbance can enhance richness in numerous ways. Predation is a factor which plays a role similar to disturbance in communities, and likewise can be considered a violation of various conditions, depending on its mode of action.

Simplification of Table 5

If resources are defined very broadly, conditions (2) and (3) can be merged with condition (4). That is, if "cool, wet microsites" is a resource, or "the time period immediately after a fire" is a resource, then 2-4 can be joined. Disturbance theory often considers "patches", which are defined spatially and temporally, as resources (e.g. TILMAN 1982).

Gause's Principle and the niche

One distinction between the reformulation in Tab. 5 and most previous definitions (Tab. 4) is that it does not rely on a rigorous concept of the niche. The Hutchinsonian niche (HUTCHINSON 1957) is perhaps the most useful definition, yet it is still wrought with ambiguity (c.f. discussion above, WHITTAKER et al. 1973, PONTIN 1982, SMITH 1990). This ambiguity is aptly described by SMITH (1990): "Niche is one of those nebulous terms in ecology, its meaning colored by various interpretations that equate it with habitat, functional roles, food habitats and morphological traits... it means an organism's place in the environment - or does it?" Given the difficulty with niche concepts, it is best to avoid building an ecological theory around them.

Limitations of the approach

Not all of the hypotheses in Tab. 1 can be considered a violation of conditions of the CEP. For example, the sampling artifact hypothesis predicts higher species richness where there are more individuals present, simply because the number of individuals places an upper limit on the potential number of species. Also, as previously mentioned, hypotheses which predict different sizes of the species pool (e.g. evolutionary time hypothesis, glacial extinction hypothesis) are violations of the premise, not the conditions, of the CEP.

Another apparent limitation of the approach is that many hypotheses are complex interactions of forces. For example, the resource ratio hypothesis predicts coexistence as a result of violating conditions (3) and (4). However, this is also a limitation of the HWP: any actual case of evolution is most likely a violation of more than one condition of Tab. 3.

The CEP predicts that competitive exclusion will result in a low-diversity system. This assumes that competitive relationships among species are fairly direct, and that higher-level indirect interactions among species are fairly weak. However, STONE & ROBERTS (1991) and WILSON (1992) have argued that indirect interactions often allow species to gain advantage from the presence of competitors in a community context. This might allow high-richness communities because of (not in spite of) strong competition. If such situations are common, then any approach relating species richness to the CEP is suspect.

There is a major difference between the CEP and the HWP which cautions against overextending the analogy. The HWP predicts that change will **not** take place if none of the conditions are violated, but the CEP predicts that change **will** occur. The purpose of the analogy proposed here is not to "map" the CEP onto the HWP, but to argue that the CEP can be structured in a way which has been pedagogically and organizationally useful in another discipline.

Equilibrium and the CEP

The CEP is often viewed as the central organizing concept in an equilibrium view of ecology. Over the past several decades, however, there has been an increasing appreciation that many, if not most, communities are not in equilibrium. This awareness is symbolized in a 1990 Ecological Society of America symposium entitled "The shift from an equilibrium to a non-equilibrium paradigm in ecology" (MURDOCH 1991). The title is derived from the ideas of KUHN (1970), who argues that scientific revolutions occur in times of paradigm shifts (that is, changes in world view). It is difficult to envision what a nonequilibrium paradigm could be like. This is probably because "nonequilibrium paradigm" is an oxymoron: **nonequilibrium** is a concept which only makes sense in the context of **equilibrium**, and therefore cannot be treated as an independent field of study, even if equilibrium conditions never exist (see KOETSIER et al. 1990). Perhaps the realization that nonequilibrium conditions are pervasive should not be considered a paradigm shift, but merely a shift in emphasis, part of what Kuhn considers "normal science" as opposed to "revolutionary science". Alternatively, we can view changes in ecology as a shifting of **metaphors**, as BOTKIN (1990) puts it, from the community as an organism, to the community as a machine, to something quite different, without profoundly changing our models of coexistence.

CONCLUSION

I propose modelling the CEP after the HWP of population genetics. Although the Hardy-Weinberg equilibrium probably never exists, the principle has played a formative role in evolutionary theory. Likewise, I treat competitive exclusion as a central organizing concept in community ecology, though the relaxation, disruption, or prevention of interspecific competition is probably the status quo in most communities.

CODA

It is unlikely that the huge mass of competing hypotheses, paradigms, classification schemes, etc. will be resolved any time soon. The study of coexistence is truly unique in the complexity of the proposed hypotheses and their interrelationships. GENTRY (1988) pointed out that many experts on species richness, faced with such complexity, have been forced to change their views substantially, though in quite diverse directions. In the midst of this chaos, we can take comfort by remembering another uniqueness of the coexistence problem: it is probably the only scientific endeavor which has a patron saint, Santa Rosalia (HUTCHINSON 1959).

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APPENDIX

Table 1. Hypotheses explaining coexistence or variation in species richness. The citations are examples of studies using the hypotheses by name; however, they do not necessarily represent proponents, nor the originators of the terms. Superscripts refer to the condition(s) of the competitive exclusion principle (Tab. 5) which is (are) broken or modified; "P" refers to a violation of the premise of the principle, and "?" means it is not clear which conditions are involved.

Aggregation (Hypothesis) (WILSON 1990, ATKINSON & SHORROCKS 1981)^{1,6}
Alternate Life-History Strategies (SHMIDA & ELLNER 1984)^{5}
Alternation of Species (FOX 1977)^{5}
Area (per se) Hypothesis/ Effects (NILSSON et al. 1988, HOLT 1992)^{1,3,6,P}
Balanced Competition Theory (ZOBEL 1992)^{1}
Biochemical Barrier Hypothesis (JONES & LAWTON 1991)^{7}
Cascade Effects (TSCHARNTKE 1992)^{5}
Circular (Competitive) Networks Hypothesis (WILSON 1990, AARSSEN 1992)^{2,5}
Climatic Stability (Variation) Hypothesis (Theory) (SANDERS 1968)^{2}
Common Chemistry Hypothesis (JONES & LAWTON 1991)^{P}
Compensatory Mortality Hypothesis (CONNELL 1978, GILLER 1984)^{5}
Competition Hypothesis/Theory (SANDERS 1968, GILLER 1984)^{4}
Competitive Combining Ability Hypothesis (AARSSEN 1983)^{1}
Complete Equality Hypothesis (AARSSEN 1992)^{1}
Complex Interactions (WILSON 1992)$^{?}$
Consumer Strategies (DIAMOND 1988)^{4}
C-S-R Model (TAYLOR et al. 1990)^{1,P}
Cyclic Regeneration Hypothesis (SHMIDA & ELLNER 1984)^{2,3,4,5}
Cyclic Succession Hypothesis (WILSON 1990)^{2,3,4,5}
Distance effect (WILSON & BOSSERT 1971, SCHOENER 1988)^{7,P}
Distance from Coast Model (NILSSON et al. 1991)$^{?}$
Disturbance Heterogeneity Model (COLLINS 1992)^{2,3}
Disturbance Phasing (ABUGOV 1982)^{2,3}
Diverse Defence Hypothesis (JONES & LAWTON 1991)^{P}
Diversity-Stability Hypothesis (HAIRSTON et al. 1968)$^{?}$
Dynamic Equilibrium Hypothesis (HUSTON 1979, SMITH 1990)^{2,3}
Ecological Combining Ability Hypothesis (AARSSEN 1983)^{4}
Ecological Equivalency Hypothesis (SHMIDA & WILSON 1985)^{6}
Ecological Time Hypothesis (COLLIER et al. 1973, GILLER 1984)^{P}
Edge Effect (SMITH 1990, NOSS 1991)^{3,7}
Enemy Escape Hypothesis (JONES & LAWTON 1991)^{5}
Energy Theory (COUSINS 1989, CURRIE 1991, LATHAM & RICKLEFS 1993)^{P,3,4}
(Environmental) Favourability (Favourableness) Hypothesis (GILLER 1984, BROWN 1988)^{P}
Environmental Harshness (Hypothesis) (BEGON et al. 1990)^{P}
Environmental Heterogeneity (Variability) Hypothesis (AARSEN 1992, GILLER 1984, PALMER 1991)^{3}
Environmental Stability Hypothesis (COLLIER et al. 1973)^{P}
Environment-Distance Hypothesis (MILNE & FORMAN 1986)^{3,7}
Equal Chance Hypothesis (CONNELL 1978, WILSON 1990)^{1,3}
Equilibrium Hypothesis (BROWN 1988, KELLY et al. 1989)^{4}
Evolutionary Time Hypothesis (GILLER 1984, SMITH 1990)^{P}
Favourableness-Severity Hypothesis (REAL et al. 1993)^{P}
Forest Architecture Hypothesis (KOHYAMA 1993)^{2,3,4}
Fundamental Niche Differentiation (LATHAM 1992)^{4}
Gaussian Coexistence Hypothesis (AARSSEN 1983)^{4}
Genetic Feedback (PIMENTEL 1968)$^{?}$

Glacial Extinction Hypothesis (Adams & Woodward 1989)[P]
Global Biological Constraints (Palmer 1992)[P]
Gradual (Climate) Change Hypothesis (Connell 1978, Giller 1984)[2]
Habitat Area Hypothesis (Palmer 1992)[1,6]
Habitat Change Model (Schwartz 1988)[2]
Habitat Differentiation (Whittaker 1965)[3]
Habitat Diversity (Complexity, Heterogeneity) Hypothesis (Terborgh 1977, Shmida & Wilson 1985, Brown 1988)[3]
Historical Effects (Quinn & Harrison 1988)[1,2,P]
Immigration-Extinction Hypothesis (Osborne & Wiley 1992)[7]
Incidence Function Hypothesis (Kelly et al. 1989)[P]
Initial Patch Composition Hypothesis (Wilson 1990)[6]
Intermediate - Timescale Disturbance Hypothesis (Wilson 1990)[1,2]
Intermediate Disturbance Hypothesis (Connell 1978, Huston 1979)[1,2,3,4,7]
Internal Storage Effect (Holt 1992)[7]
Janzen-Connell Hypothesis (Condit et al. 1992, Schupp 1992)[5]
Keystone Predators/Granivory (Samson et al. 1992)[5]
Life History Differences Hypothesis (Wilson 1990)[4]
Limiting Similarity (MacArthur & Levins 1967)[4]
Lottery (Establishment) (Hypothesis) (Fagerström 1988, Aarsen 1992, Lavorel & Lebreton 1992)[6]
(MacArthur-Wilson) Island Biogeography Theory (Many Hypotheses) (MacArthur & Wilson 1967)[1,2,3,6,7,P]
Musical Chairs Model (Crawley 1986)[6]
Mycorrhiza Hypothesis (Connell & Lowman 1989)[1]
Niche Breadth (Brown 1988)[4]
Niche Dimensions (Hypothesis) (Pianka 1973)[3,4]
Niche Diversification/ Differentiation/ Segregation/ Separation (Hypothesis) (Whittaker 1965, Connell 1978, Crawley 1986, Wilson 1990, Haukisalmi & Henttonen 1993)[3,4]
Niche Heterogeneity (Cornell & Lawton 1992)[3,4]
Niche Overlap (Hypothesis) (Pianka 1973)[1]
Niche Relations (Hypothesis) (Shmida & Wilson 1985)[4]
Nonequilibrium coexistence (Pickett 1980)[1]
Pest (Predator) Pressure Hypothesis (Wilson 1990)[5]
Predation Hypothesis (Theory) (Paine 1966, Sanders 1968)[5]
Priority Effects (Quinn & Harrison 1988)[6]
Probability Refuge (Haukisalmi & Henttonen 1993)[5]
Productivity Hypothesis/Theory (Sanders 1968, Brown 1988)[7]
Random Placement Hypothesis (Kelly et al. 1989)[P]
Rapoport-Rescue Hypothesis (Stevens 1992)[7]
Reciprocal Replacement (Woods 1979)[5]
Refuges (Crawley 1986)[5]
Regeneration Niche Hypothesis (Grubb 1977, Mohler 1990)[2,3,4]
Rescue effect (Brown & Kodric-Brown 1977, Stevens 1992)[7]
Resource-Fragmentation Hypothesis (Hawkins et al. 1992)[3,6]
Resource Heterogeneity (Diversity) Hypothesis (Tscharntke 1992, Szentkiralyi & Kozar 1991)[3,4]
Resource Partitioning (Crawley 1986)[4]
Resource Quality (Diamond 1988)[7]
Resource Ratio Hypothesis (Tilman 1985)[3,4]
Resource Richness - Species Richness Hypothesis (Tilman 1985)[3,4]
River Size Model (Nilsson et al. 1991)[7]
Sampling Artifact Hypothesis (Palmer 1991)[7]
Saturation Hypothesis (Zimmerman 1992)[P]
Scale Model (Nilsson et al. 1991)[7]
Seed Re-immigration Concept (Zobel 1992)[7]

Selective Herbivory (CRAWLEY 1986)[5]
Shifting Competitive Hierarchy (LATHAM 1992)[2,4]
Simpson Hypothesis (MILNE & FORMAN 1986)[7,P]
Small Island Effect (HEATWOLE 1991, KELLY et al. 1989)[1,6,7]
Small Island Habitat Hypothesis (TANGNEY et al. 1990, KELLY et al. 1989)[3]
(Spatial) Mass Effect Hypothesis (WILSON 1990, PALMER 1992)[3,7]
Spatial Variability (Heterogeneity) Hypothesis (GILLER 1984, BEGON et al. 1990)[3]
Spatiotemporal Heterogeneity (CORNELL & LAWTON 1992)[2,3]
Species-Interactive Theory of Island Biogeography (CASE 1991)[4,7]
Species-Pool Hypotheses (TAYLOR et al. 1990, REBELE 1992)[P]
Species Themselves as Niches (DIAMOND 1988)[4]
Stability-Time Hypothesis (SANDERS 1968)[P]
Stabilizing Coevolution Hypothesis (WILSON 1990)[4]
Stepping Stone Effect (HOLT 1992)[7]
Storage Effect (Hypothesis) (WARNER & CHESSON 1985)[7]
Structural Heterogeneity Hypothesis (TERBORGH 1977)[3]
Subdivision Effects (ROBINSON & QUINN 1988)[6]
Supersaturation Effect (DIAMOND 1988)[1]
Tall Poppy Hypothesis (PIMM 1991)[5]
Temporal Mass Effect (Hypothesis) (SHMIDA & ELLNER 1984)[2,7]
Temporal Variability (Hypothesis) (DIAMOND 1988)[2]
Theory of Random Placement (COLEMAN et al. 1982)[P]
Time Hypothesis (BUSH et al. 1990)[P]
Time Partitioning (LOREAU 1992)[2]