

# Community Ecology in 40,000 words or less

The following are the summaries of papers relating to PBG 200B (1998). The list is alphabetical by author. These summaries are the collected effort of the UC Davis Graduate Group in Population Biology 1997-1998 Cohort (A. Bell, K. Copren, R. Haygood, L. King, D. Lockwood, B. Spitzer, and K. Whitney).

**Axelrod & Hamilton 1981.** The evolution of cooperation. *Science* 211:1390-1396.

**One sentence summary:** “On the assumption that interactions between pairs of individuals occur on a probabilistic basis, a model is developed based on ESS and the Prisoner’s dilemma. Cooperation based on reciprocity can get started in an asocial world, can thrive while interacting with a wide range of other strategies, and can resist invasion once fully established. Potential applications include specific aspects of territoriality, mating and disease.”

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Background: post-Darwin, cooperation was never given much attention because of the assumption that group selection would produce it. Once group selection came into disfavor (and Darwin’s focus on the individual was resumed), two extensions have been developed: kinship theory (in which the gene “looks beyond its mortal bearer to the interests of its potentially immortal set of it replicas existing in other related individuals”) and reciprocation theory.

The Prisoner’s dilemma:

	B cooperates	B defects
A cooperates	R = 3 reward for coop (neither narcs)	S = 0 sucker’s payoff
A defects	T = 5 tempt to defect	P = 1

The game is defined by  $T > R > P > S$  and  $R > (S+T)/2$

When played only once or with a known number of encounters, no strategy can invade the ALL DEFECT strategy. When played with a probability  $w$  of repeat encounters, TIT FOR TAT is

robust - meaning it goes to fixation in an environment of many competing strategies

stable - meaning it is non-invasible once it is fixed (Ralph says this is not true, can be invaded by ALWAYS COOPERATE, which has the same success, via drift)

The problem is that TIT FOR TAT is not initially viable (cannot invade ALL DEFECT). Two mechanisms are suggested that could jump start it: kinship and clustering. Kinship alters the payoff matrix because (from a gene’s perspective) you have a stake in your partner’s success. In clustering, a small group of TIT FOR TAT players have a higher probability of interacting with themselves than with the population at large, and gradually invade.

Requirements for the evolution of cooperation:

- 1) Probability  $w$  of interaction must be sufficiently high
- 2) Player must be able to retaliate against defection - requires recognition

**Baldwin et al. 1990.** The reproductive consequences associated with inducible alkaloidal responses in wild tobacco. *Ecology* 71:252-262.

Alkaloid production was decoupled from leaf damage by a) treatment with auxin or b) damage that avoided veins, both of which stopped induction. Thus, they had two groups of plants, both with equal biomass removed but only one producing increased alkaloids. This was factored over rosette-stage and flowering-stage plants. Seed set

measured.

Plants damaged during the rosette stage were able to fully compensate (matched seed set of undamaged plants; no cost of biomass removal or induction). In flowering plants, full compensation was not achieved, and alkaloid-producing plants had fewer seeds than those in which induction was prevented (both biomass removal and induction had costs).

This is consistent with a cost of induction; supported by the observation in undamaged plants that constitutive alkaloid content was negatively correlated with seed set. However, authors state that this is a phenotypic cost and may not be directly related to alkaloid production (other unmeasured responses to damage may accompany the alkaloidal response).

**Bengtsson, J. (1991)** Interspecific competition in metapopulations. *Biological Journal of the Linnean Society*. 42:219-237

**One sentence summary:** Interspecific competition is important for the distributional dynamics of *Daphnia* spp. in rock pools, but whether the coexistence of these species depends on metapopulation dynamics is unresolved.

Don put this paper on his list as an example of a paper on how spatial heterogeneity could be one of the factors maintaining biological diversity. Multi-species metapopulation models have been constructed to investigate the conditions under which spatial heterogeneity allows the coexistence of competitors that would not coexist in a homogenous environment. The benefit of this paper is that it is relatively recent (1991) and provides a review of other empirical studies on this topic. However, the main question is not conclusively answered. The important point here is that spatial heterogeneity is a regional argument rather than a local argument for the maintenance of diversity. Biological diversity can be maintained by a balance of extinctions and colonizations on the local level, which create the regional dynamics.

Bengtsson explains the assumptions and predictions of metapopulation models for competing species. First, he uses his own system, *Daphnia* in rock pools, to test these predictions. Then he reviews the literature and compares other empirical work to these predictions and assumptions. There are two ideas here: 1) determining if competition exists and 2) if spatial heterogeneity allows the maintenance of competitors on the regional scale. He concludes that in three species of *Daphnia* in rock pools, interspecific competition increased local extinction rates, while no effects on colonization rates were detected. Distributional patterns were consistent with several predictions of the competition model; for example, the number of species on an island increased with the number of pools and the proportion of pools occupied by each species decreased with increasing species number. He concludes that interspecific competition is important for the distributional dynamics of *Daphnia*, but whether their coexistence depends on metapopulation dynamics is still unresolved.

Reviewing the literature, he finds that empirical studies done to date are not directly relevant to the question of coexistence. These studies, not asking the same questions about the model, do not necessarily evaluate competition between the organisms being studied. Even if interspecific competition influences colonization and extinction rates in such systems, the explanation for regional coexistence may still be niche differences. Many metapopulations may be of the mainland-island type, with different species having different mainland patches. He states that critical experimental tests have not been conducted in any field system to demonstrate that metapopulation structure per se allows species to coexist. He thinks that the type of study he did with *Daphnia*, i.e. looking directly for interspecific competition, needs to be evaluated in other systems.

**Benton, M.J. (1995)** Diversification and extinction in the history of life. *Science*, 268: 52-58.

**One sentence summary:** There appears in the fossil record to be no upper limit to diversity on the planet.

Benton analyzes the fossil records of ALL life, and finds that diversity of both marine and continental life increased exponentially since the end of the Precambrian. This diversification was interrupted by mass

extinctions which were experienced most of the time by both marine and continental organisms. The importance of this paper is short and sweet: There appears no limit to diversity in the fossil record. Although this paper is found under the topic of mutualism it is important to both competition and mutualism theories. If there is no limit to the amount of diversity, it reduces support for both the idea of competition and mutualism having an effect on global (scale important) diversity. There is no apparent influence of intimate mutualisms effecting this pattern, according to DRS. This comes in contrast to the idea that insect/plant mutualism provided positive feedback for diversification (Regal 1977). Also, it suggests that species number is not limited by competitive exclusion, at least globally. So is the earth “undersaturated”? These ideas are given by Don as conclusions to this paper, none are stated in the paper.

**Berlow, E.L.** 1997. From canalization to contingency: historical effects in a successional rocky intertidal community. *Ecological Monographs* 67: 435-460.

**One sentence summary:** succession is a historical process, so how do past events create current variation in community structure and organization? Do successional changes dampen, track or magnify extrinsic variation? Take home: all forces operate at some level, question is which ones where?

The system: rocky intertidal in Oregon

Definitions:

Canalized succession: consistent effects of early events, deterministic, repeatable process.

Externally driven succession: extrinsic events drive stochastic variation

Contingent succession: if sign and magnitude of species interactions depend on context in which they occur.

Stochastic + deterministic (contingent)

Methods: cleared patches to mimic disturbance, at yearly intervals to test for the effects of year (starting date: when patch cleared), successional age (time elapsed since cleared), and census year (when plot observed). Massive ANOVA to determine importance of these under three different predator densities.

Results: different types of succession for different species, different mechanisms operating simultaneously. The results were really complicated – historical effects varied among species and between different stages of succession. However, there were some consistent and repeatable patterns, e.g. progression from small to large species. Some noise-dampening (canalizing) forces (facilitation, competition and predation), some noise amplifying forces (including indirect effects, prey refuge).

**Bertness & Calloway** 1994. Positive interactions in communities. *TREE* 9:191-193.

“Whereas the ecology and evolutionary biology of mutualisms has attracted recent attention, the role that they play in the structure and organization of natural communities has not.” They are seen as anecdotal stories rather than as major forces; are absent from models and from textbooks. While positive indirect effects and feedbacks in foodwebs are important, the focus here is on non-trophic interactions. These interactions affect recruitment, species distributions, and succession. Examples:

1) Primary space-holders facilitate recruitment

nurse plants in deserts

salt marsh plants reduce salinization (see Shumway & Bertness 1994)

2) species distributions

the upper intertidal limits of algae and sessile invertebrates have been shown to be positively effected by group benefits of thermal and desiccation buffering.

3) succession

salt marsh plants reduce salinization (see Shumway & Bertness 1994)

algae facilitate seagrass colonization of sand substrates via nutrient addition forests are probably another example, but we don't see facilitation if we look at too small a scale (we see competition). [E.g. Oaks and maples may compete on small scale, but perhaps on a larger scale (outside the forest in the open) maples may not be able to est. at all. This is just my hypothetical speculation.]

Mechanisms: primary space-holders frequently buffer neighbors from potentially limiting stresses e.g. heat/desiccation, low nutrient levels, osmotic stress, soil oxygen, soil moisture, disturbance. This is why positive interactions are most noticeable in harsh environments like deserts & salt marshes.

Stupid graphical model: Across communities, at extremes of "consumer pressure" and/or "physical stress", positive interactions are more likely to be found. At intermediate levels competition will dominate. At high "physical stress" neighborhood habitat amelioration will be the mechanism, while at high "consumer pressure" associational defenses will be it (e.g. living with less-palatable neighbors). Ken says: Why do we keep building graphical models like this with unquantifiable axes? "Stress" is measured by how the environment affects organisms, so you cannot compare "stress" levels across communities of differing species composition.

**Bowers 1993.** Influence of herbivorous mammals on an old-field plant community: years 1-4 after disturbance. *Oikos* 67:129-141.

Another hump-shaped distribution.

An old field in Virginia was sprayed with herbicide then plowed. Enclosures to keep out herbivores of different sizes. At intermediate levels of herbivory (some, but not all, size-classes of herbivores excluded), plant diversity was the highest. At high (no herbivores excluded) or low (all mammalian herbivores excluded) levels of herbivory, diversity was low. Total cover was lowest in control plots (no herbivores excluded). The main effect of herbivory appears to be in altering competitive hierarchies among the plant community rather than by directly causing plant mortality.

**Bowers, M.A. 1993.** Influence of herbivorous mammals on an old-field plant community: years 1-4 after disturbance. *Oikos* 67: 129-141.

**One-sentence summary:** Some species are hit disproportionately hard by herbivores; others benefit, apparently because their competitors are being suppressed. The net outcome is a sort of "intermediate herbivory hypothesis": a moderate level of herbivory balances competitive exclusion and leads to a maximal species diversity.

The author wiped out an old-field community with herbicide and tilling and monitored fenced plots while it regrew from the seed bank and seed rain. The fences around the plots were designed to exclude 1) all mammalian herbivores, 2) large and medium-sized herbivores (deer, woodchucks, and rabbits), 3) large mammalian herbivores only (deer), or 4) nothing. Because these herbivores generally had the same plant preferences, these treatments turned out to reflect four levels of grazing intensity. In general, rapid-growing, tall plants (good competitors) were most reduced by herbivory. The outcome is much like Connell's (1975) intermediate disturbance hypothesis, which proposes that intermediate levels of disturbance maximize community diversity. Bowers notes that, because each species may respond different to herbivory, this result is not necessarily general across systems. It is not clear how herbivory is affecting succession in this community; the effects of herbivory can interact with a number of other factors and can potentially accelerate or inhibit succession depending on these interactions.

**Brett, M.T. and C.R. Goldman (1996)** A meta-analysis of the fresh water trophic cascade. *PNAS* 93: 7723-7726.

**AND(1997)** Consumers versus resource control in fresh-water pelagic food webs. *Science* 275: 384-386.

#### 1996-Meta-analysis

**One sentence summary:** Quantitatively summarizes 54 experiments measuring the response of the zooplankton and phytoplankton to zooplanktivorous fish treatments, and unequivocally supports the ATC hypothesis in freshwater food webs.

They summarized quantitatively 54 separate enclosure and pond experiments that measured the response of the zooplankton and phytoplankton to zooplanktivorous fish treatments. Showed that in general the

zooplanktivorous fish treatments resulted in greatly decreased zooplankton biomass. Similarly, the fish treatments resulted in increased phytoplankton biomass. Provides unequivocal support for the ATC hypothesis. In 52/54 studies summarized zooplankton biomass was depressed by zooplanktivorous fish treatments, whereas in 51/54 cases these same treatments increased the biomass of the phytoplankton. However, in many cases, these effects were small, particularly for the phytoplankton, and would not be statistically detected by a study with no or few replicates and high variability (two thirds showed weak responses and one third showed strong responses). Even though, on the whole, phytoplankton increased in the presence of zooplanktivorous fish, this effect was NOT as strong as expected. In some studies it wasn't even seen. This is what Don refers to as a trophic "trickle" instead of "cascade" because a much smaller effect is seen in the phytoplankton. Something else must be going on with the phytoplankton. The lack of effect in some studies has generated some people who do these treatments to reject the ATC. This paper, however, should resolve the debate over whether the trophic cascade is a general feature of freshwater food webs. Rather, attention should be focused on explaining variation in the response of phytoplankton to the cascade.

#### 1997-Consumer vs. resource

**One sentence summary:** Zooplankton biomass is under strong consumer control but is weakly stimulated by nutrient additions; phytoplankton biomass is under strong resource control with moderate control by fish.

This is the follow-up to the above paper attempting to look at the variability in phytoplankton response to zooplanktivorous fish. Once again they conduct a meta-analysis of 11 fish(consumer)-by-nutrient (resource) factorial plankton community experiments. The debate centers on whether herbivore and plant communities are regulated through predator control of herbivore abundance or through nutrient control of primary production. Tests McQueen's hypothesis (see this paper for reference) that predict bottom-up control is stronger at the base of the food web, and top-down control is stronger at higher trophic levels. Also tests Oksanen's (1981) prediction that says in food webs with an odd number of trophic levels, increases in primary production should lead to increased biomass for odd-numbered trophic levels and no change in biomass for even-numbered trophic levels. Conversely, in food webs with an even number of trophic levels, increases in primary production should lead to increased biomass for even-numbered trophic levels and no change in biomass for odd-numbered trophic levels. Their analysis provides strong agreement with McQueen. They found top-down control had a much stronger impact on zooplankton biomass than did bottom-up control. They found both top-down and bottom-up control of phytoplankton community biomass with bottom-up control stronger than top-down.

Their analysis did not support Oksanen *et al.* According to Oksanen's prediction, in a two trophic level food web, increases in primary production would result in increased zooplankton biomass and no change in phytoplankton biomass. They found that in this case (one link, phytoplankton and zooplankton) nutrient addition caused large increases in phytoplankton density and little increase in zooplankton density. Oksanen predicts that in three trophic level food webs, increases in the system primary production would result in increased phytoplankton biomass and no change in zooplankton biomass. They found that in this case (two link, phytoplankton, zooplankton, and planktivorous fish) nutrient addition caused even less increase in zooplankton. Their results suggest that, under certain conditions, increased primary production due to nutrient inputs may not be efficiently transferred to herbivorous zooplankton biomass.

**Bronstein 1994.** Our current understanding of mutualism. *Quarterly Review of Biology* 69:31-51.

**One sentence summary:** a review of all articles appearing in 9 ecology/evolution journals from 1986-1990 determines that, contrary to widespread belief that mutualisms have been grossly neglected relative to their true importance in nature, we have accumulated tons of data on them. In fact, they are studied at least as frequently as competition, though less so than predation. However, this data remains as isolated case histories. Researchers have treated mutualism primarily as a life history attribute of one of the two partners, rather than as a form of interaction in the same way as studies of competition or predation.

3 major obstacles to deriving general principles of mutualism:

- 1) certain mutualisms (e.g. pollination) have become isolated fields, each w/ unique focal questions & methodologies
- 2) there is little connection between theory of mutualism and empirical tests
- 3) mutualisms are usually studied from the perspective of only 1 of the partners

8 questions are identified as “emerging directions” in mutualism research:

- 1) are mutualisms delicately balanced antagonisms?
- 2) how common are mutualisms involving asymmetrical dependence; when and where do they occur?
- 3) Where are we most likely to see a tight match between mutualist traits, and what processes can produce it?
- 4) When are the costs and benefits within mutualisms context dependent?
- 5) Is there positive feedback in mutualist population sizes?
- 6) How much do individual species invest in the different forms of mutualism in which they are involved? [eg, trade-offs between pollen prod., fruit prod., shunting of photosynthate to mycorrhize]
- 7) How are within-species and between-species cooperative interactions similar and different?
- 8) How common are cheaters in mutualistic systems; where and when do they occur?

States that most types of services and rewards are known, and “new” types of mutualisms appearing in the literature are those in which the identity of the service provider is unexpected (e.g., seed dispersal by fish).

**Bull, J. J., and Rice, W. R., 1991.** Distinguishing mechanisms for the evolution of cooperation. *Journal of Theoretical Biology* 149:63-74.

**One-sentence summary:** Two mechanisms for preventing an interspecific cooperation system from being destabilized by cheating are distinguished: partner-fidelity, where iterated interactions between pairs of individuals mean that uncooperativeness in one interaction may incur retaliation in another, and partner-choice, where a member of one species chooses the most cooperative one of several members of another species; the iterated prisoner’s dilemma embodies partner-fidelity, and the yucca/yucca moth mutualism exemplifies partner-choice.

This article calls attention to a distinction between two kinds of interspecific cooperation system. (In principle, the same considerations apply to cooperation within species, but this article does not pursue this point.) The distinction lies in how a system overcomes destabilization by cheating, which the authors consider the main obstacle to the evolution of cooperation. (According to the authors, “If cooperation is to be evolutionarily stable, then, uncooperative behaviors must be \*individually\* penalized or retaliated” (p. 64), but on the basis of experiments with an iterated three-player prisoner’s dilemma, I doubt this is necessary.) In what the authors term partner-fidelity systems, “life histories of the interacting species exhibit repeated or long-term interactions between the same individual partners---high partner-fidelity.” (p. 65) In such a situation, uncooperativeness in one interaction may incur retaliation in another, stabilizing cooperation. The paradigmatic model of this kind is the iterated prisoner’s dilemma (IPD), as reviewed by Axelrod and Hamilton, 1981. Bull and Rice propose their own simple model of iterated interactions, with degrees of both cooperation and partner-fidelity continuous variables. This yields a relation between the degree of cooperation favored by selection and the degree of partner-fidelity assumed. They also mention some biological phenomena that can be interpreted in terms of such models. Perhaps the most striking is the evolution of virulence in microparasites as a correlate of transmission mode: the authors suggest that vertical transmission, which promotes benignity, can be regarded as a kind of partner-fidelity.

In contrast, in what the authors term partner-choice systems, “an individual of species A is paired with several members of species B for a single interaction, but A chooses to reward only the most cooperative members of B.” (p. 68) Their main examples are the fig/fig wasp and yucca/yucca moth mutualisms. E.g., the flowers on a yucca may be pollinated and oviposited in by many moths, hence potentially the plant can preferentially ripen fruits where the fewest eggs are laid, aborting fruits associated with the most selfish moths; since this article was written, Pellmyr and collaborators have shown this possibility is realized. Bull and Rice point out that although Axelrod and Hamilton, 1981 discusses the fig/fig wasp mutualism, such a situation differs from an IPD-like situation in that there need not be iterated interactions between pairs of individuals in order for cooperation to be stable---maybe. The ‘maybe’ is because such a situation offers scope for a kind of evolutionary arms race, with species B (the chosen) selected for ability to deceive species A (the one who chooses) and species A selected for ability to discriminate against deception by species B. E.g., cheater moths oviposit in yucca ovaries subsequent to the temporal window in which the plants’ selective fruit abortion system operates; under the circumstances, one expects the window to lengthen and/or the plants to develop direct egg and/or larva poisoning mechanisms. The authors propose no model

that could be paradigmatic for partner-choice systems as the IPD is paradigmatic for partner-fidelity systems.

**Carpenter, S. R., K. L. Cottingham & D. E. Schindler.** 1992. Biotic Feedbacks in lake phosphorus cycles. *Tree* 7(10): 232-236.

**One sentence summary:** In lakes the nutrient cycles are influenced greatly by the ATC interactions.

The primary producers of lakes (cyanobacteria and algae) are limited by N and P (at different levels for various species). The source of most of the nutrients in lakes appears to be contained in the cycling of these nutrients through the zooplankton and fish populations (as well as the detritus). This is very different from terrestrial systems in which the inorganic nutrients do not have large pools in the higher levels of the trophic structure. Zooplankton can alter the limiting factor and as such influence the dominance of the bacteria (which fix N and have an advantage in N-limited environments) and algae (which have an advantage in P-limited environments). The planktivorous fish can alter the abundances of zooplankton which can result in changes of the N and P loads.

The stability (resistance and resilience á la Pimm) of nutrient cycles (and hence ecosystems) is affected by the nutrient input. Thus fish can influence the stability of the system via direct predation and by nutrient cycling. Thus restoration work in lakes is more complex due to the variety of interactions and feedback mechanisms.

**Carpenter, S.R. & Kitchell, J.F.** 1988. Consumer control of lake productivity. *BioScience* 38: 764-769.

**The main point:** aquatic trophic cascades in whole lake ecosystems. This is a very general summary of a complicated system.

**The system:** four lakes in Wisconsin subject to different experimental treatments monitored for four years. The main experiment was a comparison between two lakes (with and without piscivores).

(piscivores) ← planktivores ← herbivores (daphnia) ← phytoplankton

These trophic levels are distinct, as they represent only one species.

**Methods and results:** Reciprocal transplant experiment where piscivores from one lake were transferred to the other while planktivores were transferred from the other. This long(er) term study saw the effects of removal/addition over time, but the effects were not immediate! Basically, the long term results was as follows: when piscivores were removed, planktivores went up, herbivores went down and phytoplankton went up (green lake). When piscivores were added, planktivores went down, herbivores went up and phytoplankton went down (blue lake). Let me just say that the process of getting to this result was much more complicated, with differences in time scales between the two lakes, changes in body size over time, changes in prey types with maturity etc.

They also reported results from an enclosure experiment, which revealed the short-term regulation of phytoplankton. "The distinction between enclosure and whole lake responses is analogous to that between short term processes that maintain community structure and long term processes that establish community structure."

**Interesting things:** This study verifies the important role of predators and offers support for HSS: the world is green because of predation on herbivores. However, the world is blue if top predators eat herbivore predators!

This paper emphasized that trophic cascades and physicochemical factors may both be important in determining lake dynamics, but they may operate at different time scales to determine lake productivity, and their relative effects may vary depending on those time scales. Re: top down versus bottom up: "How much and when?". Processes that govern lake productivity may operate at different time scales: nutrient and hydrological processes operate on scales of decades to centuries, trophic cascades may vary at a scale of years to decades (depending on life span of top predators), whereas weather may operate at subannual, daily or weekly time scales. The authors argue that these differences in time scales, as well as dynamic oscillations often found in predator prey dynamics, make long term experimental lake studies robust. This paper is hard to summarize because it is a summary of gobs and gobs of work and data. I recommend it, however, as an overview of this model ATC system.

**Chapin, Walker, et al.** 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska.

Primary succession studied over a series of sites uncovered by tidewater glacier retreating northward (pioneer site

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approx. 15 yrs old, Dryas site 30-40 yrs, alder site 60 yrs, spruce site 200 yrs). Dryas and alder are N-fixers.

Pioneer (0-20 yrs): "black crust" of blue-green algae, *Equisetum* gametophytes, lichens, liverworts. Scattered forbs (*Epilobium*), willows, cottonwood, spruce

Dryas (30-50 yrs): continuous mat of Dryas (mountain-avens) with scattered trees

Alder (50-100 yrs): alder forms thickets, Dryas disappears

Spruce (100+) : spruce overtops alder

Muskeg (after "1000's of yrs"): Sphagnum

Each stage enriches the soil organic matter and N content, facilitating the growth of the later species. Vegetation in each stage also inhibited germination and initial est. of sown alder and spruce seeds. However, unlike their earlier studies of primary succession on floodplains, net effect of alder on spruce is facultative.

Just as in their earlier studies of primary succession on floodplains, no single factor fully accounts for this primary succession: life history traits, competitive interactions, and facilitation are all critical. Without facilitation, the same successional sequence would happen but much more slowly; without competition, more quickly (but Dryas and alder might remain in the understory for longer).

This study took place on E. arm of Glacier Bay. On W. arm, succession also passes shrub -> tree but it is willows rather than alders. Rate is also slower. Demonstrates that succession is not deterministic even w/in relatively small area of similar abiotic conditions (although they do list some differences, eg more bedrock).

**Chesson, P.** 1991. A need for niches? *TREE* 6:26-28.

**The main point:** In this article, Chesson hits us over the head with the idea that competing species must be ecologically distinct (inhabit different niches), in order to coexist. Folks have suggested that stochastic factors, clumping, etc. may mean that niches aren't necessary for coexistence but Peter makes it abundantly clear that this is not the case. He looks at two models in particular: 1. Hubbell á la competitive equivalence and 2. The lottery model for ecologically identical species.

A definition... Niche: species-specific response to the environment.

Let's start with Hubbell... species are identical and coexistence is not indefinite; extinctions occur but they take a long time. There is not long term stability. This model does not satisfy the invasibility criterion because an individual gains no advantage of belonging to one species or another, as they are all identical, so there is no reason to suppose that individuals from the rare species will do any better than the more abundant species, eventually leading to the elimination of the more rare species!

The lottery model: there is a stable long term coexistence if species differ in their responses to the environment. Stability is satisfied by the invasibility criterion. This means that a species at low density has an average long term advantage in per capita population growth. The lottery model assumes that space is allocated to juveniles by chance processes. In the identical species model, the probability that any juvenile is successful in gaining the space needed for maturity and reproduction is inversely proportional to the density of competing juveniles. Relative recruitment from different species fluctuates over time due to stochastic fluctuations in birth rates and survival. Even in the lottery model, long term stable coexistence is not possible UNLESS the species are not identical. The lottery model does imply that similarities between species favors coexistence.

Note: even Hubbell's model of competitive equivalence assumes that species must have the ability to recognize individuals of the appropriate species and respond differently to conspecifics than heterospecifics with respect to mating so technically the species can't be completely identical... Note that the need to recognize mates also results in a low density disadvantage because at low density, there are fewer conspecifics, hence harder to find a mate.

**Chesson, P. & Huntly, N.** 1989. Short-term instabilities and long-term community dynamics. *TREE* 4:

293-298.

**The main point:** The combined short-term unstable dynamics of many species may contribute to the long-term stability of communities. That is, the community may be stable over a long period even if the constituent species' dynamics are unstable.

Some definitions:

Long-term stability - the tendency of a community to recover from extreme perturbations of the densities of any of its component species. That is, any species' abundance will show a long-term increase following a perturbation to low density.

Short term instability - trends on short time scales may lead to extinctions if extrapolated into the future. That is, species abundance decreases from low density situations.

Storage effect – refers to the fact that long lived life history stages, e.g. adults, dormant seeds, cysts or other resting stages, buffer population decline under unfavorable environments or competitive conditions.

Short and long-term dynamics linked by:

1. covariance between environment and competition. In a favorable environment, a species experiences increased competition (this means that the effects of a good env are offset by increased competition)
2. differential responses to the environment  
species differ in their responses to the environment – the optimal env differs for each species
3. subadditive growth rates – combination of relatively poor env and high competition cannot eliminate the gains achieved under good env and low competition  
the effects of competition are weaker in an unfavorable environment – comes about from traits which buffer the effects of harsh env and competition, e.g. seed banks  
this prevents the population gains during favorable conditions from being eliminated by poor conditions

Selection should favor specialization, e.g. seed banks, which allow recovery from low densities

Superadditive effects – poor conditions can more than eliminate the gains of good conditions in such a way that inverse frequency dependence and competitive exclusion result from fluctuating env - amplify population declines under unfavorable environments and competition → may lead to instability

Nonlinear effects of competition for different species may also favor stability

Environmental variability only favors long term stability if

1. non-additive OR
2. nonlinear (IS THIS RIGHT???)

(Competitive differences in variable environments are not sufficient to prevent competitive exclusion)

Long term stability

1. positive relationship between environment and competition (subadditivity)
2. buffering against environment and competition (the storage effect)
3. population growth rate is a nonlinear function of competition

**Chesson, P. & Huntly, N.** 1989. Short-term instabilities and long-term community dynamics. *TREE* 4(10): 293-299.

**One sentence summary:** Long term stability can be a consequence of short term instabilities, where if the short term dynamics were to continue, extinction would result.

Key factors in linking short- to long time scale behavior:

1. Covariance between environment and competition. Increase in environmental favorability for abundant species results in increased competition. Thus better conditions are offset by some degree by more competition.
2. Differential responses to environment. Species respond differently to the environment. Thus at low density, environmental favorability is not affected as much by competition.
3. Subadditive growth rates. Weaker effect of competition in unfavorable environment compared with favorable environment is subadditivity. This implies population growth is buffered against joint bad environment/competition and is strong with joint good environment/competition.

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Long term stability can be provided with short term harsh conditions if under low densities, the average growth rate is positive. This leads to temporal niches, but survival requires subadditivity so that gains under favorable conditions are not eliminated by poor conditions later. Although one species may be, on average, competitively dominant, each species must be dominant under some environmental conditions.

If environment and competition are superadditive and covary positively then competitive exclusion is the outcome. Long term stability can occur with negative covariance.

This parallels Grubb's "regeneration niche" (which maps to the environmental favorability here) and his non-equilibrium processes map to short term instabilities.

Some examples may occur in nature, but it has yet to be conclusively shown.

**Chesson, P. & Huntly, N.** 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am Nat* 150: 519-553.

Do environmental fluctuations necessarily enhance species diversity? No. Does harshness always decrease competition between species? No. Harshness has a direct negative effect on population growth that must be compared with the positive effects of lowered competition. Part of the confusion is that we keep thinking of spatial equilibrium, where species densities' remain constant over time. Environmental fluctuations can provide temporal niche partitioning.

**Model:** variation on Lotka Voleterra in a variable environment. Make  $r$  a function of both the "competitive response" and an "environmental response".

$$r(t) = E(t) - C(t)$$

**Conclusion:** harsh and fluctuating conditions have severely limited roles in the maintenance of diversity. Change in relative abundance depends on AVERAGE environmental response and is independent of fluctuations about these averages. Interesting result from simulations: competitive exclusion takes place independently of magnitude of competition, independent of fluctuations. Harshness cannot alter the conclusion that there must be a competitive dominant that drives the other species to extinction. Harshness can, however, alter the rate at which exclusion is approached and can alter the dominance ranking in the system (who outcompetes whom). New variables: sensitivity of growth rate to competition and sensitivity of growth rate to harshness. Species' sensitivity to competition and harshness determines if fluctuations will allow more diversity (by preventing interspecific competition).

**Interesting variation:** incorporation of nonadditivity (growth rate depends on competitive response - environmental response + combined effects of competitive and environmental response).

$$r(t) = E(t) - C(t) + \_E(t)C(t)$$

Ex: pops in which juveniles and adults are sensitive to different degrees to effects of environment and competition. These deviations from additivity allow stable coexistence!

**Chesson, P. & Rosenzweig, M.** 1991. Behavior, heterogeneity and the dynamics of interacting species. *Ecology* 72: 1187-1195.

**The main point:** behavior can affect population dynamics by introducing nonlinear density dependence or by causing nonadditivity (interaction between environmental and density-dependent processes). Behavioral responses to environmental variation can link heterogeneity and population dynamics.

Some potential behaviors with population-level consequences: mate choice, habitat selection, oviposition, feeding behavior (including predator avoidance behavior, handling time, searching, switching etc).

Some examples:

Type II functional response (handling time) adds inverse density dependence to prey population dynamics (it increases prey per capita growth rates as a function of prey density). → destabilizing

Type III functional response is a product of different behaviors. Adds positive density dependence at low prey densities because predation causes reductions in per capita growth rates as prey density increases until the effects of handling time become overriding. → stabilizing

Switching behavior (predator switches prey when prey at low density) – positive frequency dependence of functional responses, potentially promotes coexistence of prey species.

Aggregation: e.g. spatial variation in host density can lead to heterogeneity in risk if parasitoids aggregate in response to local host densities. → stabilizing

Antipredator behavior: e.g. habitat selection or movement → stabilizing

Behavior can add nonadditive growth rates: subadditive rates result from dormancy, e.g. Brown's dormant rodents (this is the same as the storage effect).

**Chesson, P.L. & Case, T.J.** 1986. Overview: Nonequilibrium community theories: chance, variability, history and coexistence. In *Community Ecology*. J. Diamond & T.J. Case (eds). Pages 229-239. Harper & Row.

**The main point:** compare different nonequilibrium theories with traditional equilibrium theory. Stable equilibrium theories mean that the structure of communities is predictable. What about nonequilibrium theories? If a community has nothing like a stable equilibrium point, can it have predictable properties, or will its structure be dominated by chance factors and historical effects?

Equilibrium theories of community structure:

Classical competition theory (Hutchinson) -

>= n limiting resources are required for the coexistence of n species. Limiting similarity: to coexist, the n species must be sufficiently dissimilar in resource use (use resources in dissimilar proportions)

Equilibrium predation –

>= n limiting factors are required for coexistence of n species (predator = limiting factor).

Equilibrium spatial variation –

n different equilibrium for each of the n patches. Environment favors different species in different patches.

Problem with traditional theory: Hutchinson observed (paradox of the plankton) that many species were coexisting on few resources. Proposed temporal variation to explain.

Nonequilibrium – where species densities do not remain constant over time at each spatial location.

Stable community – defined by: community conservation (# species remains constant), community recovery (community will recover from events that drive any of the species to low density), community assembly (community can be built up by immigration), irrelevance of history (no effect of past abundances of species)

Stable does not = equilibrium.

New theoretical directions (nonequilibrium theories):

1. Fluctuations and continuous competition – fluctuations occur in the competitive rankings of the species. Stochastic variation in environment. Differences in life history, physiology and behavior may explain coexistence. Species must differ for coexistence.
2. Fluctuations and discontinuous density-dependence or competition – fluctuations in environmental factors reduce the densities of several potentially competing species to levels where competition is weak and population growth rate is insensitive to density. Species must differ for coexistence.
3. Changing environmental mean – the mean and variance of environmental fluctuations relative to the speed of community dynamics. Slow changes – short-lived animals may track environmental changes. May see time lag in some species. History becomes important (the present community cannot be explained simply by studying it today). Hard to study.
4. Slow competitive displacement – Hubbell & Foster. Identical species. Only reproductive incompatibility provides an ecological distinction between individuals of different species. Random walk; the densities of any species are just as likely to increase as decrease – species go extinct from random drift in numbers. Diversity maintained by speciation and immigration.

**Coley, Bryant, & Chapin** 1985. Resource availability and plant antiherbivore defense. *Science* 230:895-899.

The Resource Availability Hypothesis (an alternative to Feeny's apparency hypothesis for explaining levels of defenses). Where resource availability is low, plants are selected for slow growth rates and high levels of chemical defense; where high, plants are selected for high growth rates and low levels of chemical defense. Herbivores have been shown (eg McKey & Gartlan's Cameroon work on Colobus) to much prefer fast-growing, low defense plants over slow-growing ones. While the R.A. and Apparency hypotheses often produce the same prediction, they can be decoupled; e.g. McKey & Gartlan's work showing that tree species on nutrient-poor soils contain 2x the phenolic compounds as species in similar veg. on rich soils (equal apparency, but different R.A., so R.A. hypothesis wins via explanatory power).

	Fast-growing species	Slow-growing species
resource availability	high	low
max photosynthetic rates	high	low
dark respiration rates	high	low
leaf protein content	high	low
leaf lifetime	short	long
successional status	often early	often late
rates of herbivory	high	low
amount of defense metabolites	low	high
type of defense	qualitative	quantitative
	e.g. alkaloids, glycosides	e.g. terpenes, tannins
N [] in defense metabolites	high	low
mobility of defense	high	low
turnover of defense	high	low

When you keep leaves a long time, it makes sense to produce costly metabolically inactive compounds that don't degrade quickly. These are "immobile" in the sense that they do not break down easily & cannot easily be reabsorbed before leaf abscission. They have low maintenance costs & thus represent a fixed investment.

When you drop leaves quickly, low concentrations (= low cost) of defensive compounds make sense. They are metabolically active, meaning re-absorption can take place. They have high maintenance costs.

Slow-growing plants are inherently slow-growing; even with enrichment they grow slowly. Conserve limited resources by not shedding twigs & leaves readily. Fast-growing plants have high rates of leaf turnover (since photosynthesizing ability decreases with leaf age, energy is maximized by rapid leaf turnover, even at the cost of dropping C and N in old leaves).

Interesting side point: because P is limited in almost all environments, there are no P-based defenses. The effectiveness of organophosphate pesticides probably results from their novelty to herbivores.

**Colinvaux et al. 1996.** A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* 274: 85-87.

**One sentence summary:** refugia hypothesis not supported for Amazonia.

A pollen core from a lake in NW Brazil. Over the past 40,000 yrs, the site was continuously occupied by rainforest; savannas and/or grasslands were not present during the last glacial maximum (little grass & herb pollen). The authors state that "the data suggest that the western Amazon forest was not fragmented into refugia in glacial times." Glacial age forests had similar composition to modern forests but included cool-adapted, higher-elevation species (e.g. Podocarpaceae), indicating a cooling of 5-6°C.

**Colinvaux, P.A., P.E. De Oliveira, J.E. Moreno, M.C. Miller, M.B. Bush (1996)** A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science*, 274: 85-88.

**One sentence summary:** The refugia hypothesis explaining the latitudinal gradient is disproved; during glacial times the Amazon did not dry out as shown by the preponderance of pollen from rain-forest trees rather than grasses in a sedimentary lake bed.

According to the refugium hypothesis, during glacial times the Amazonian climate dried out, favoring grasses and herbs over trees. Isolation is a classic means of speciation, so the idea was that many species arose in the resulting fragments of forest- “moist islands in a sea of aridity.” This is the mechanism that Don calls a “species pump,” a way in which the tropics can generate lots of species in comparison to higher latitudes. Most maps of presumed ice-age refugia, inferred from present-day biodiversity hot spots call for dry savannah around Lake Pata, the site of the study. So the theory predicts that in the lake’s bottom muds more than 15,000 years old, there should be less pollen from rain-forest trees and more from grasses. Instead, throughout the lake Pata record, 70% to 90% of the total pollen was from trees, with only a few percent from grass; all herb pollens remained below 10%. The hypothesis failed because it said that the Amazon was dry in the last glacial maximum. According to these results it was not. There is little evidence for refugia now, although this was once a strongly held dogma. However, some people worry about over interpreting a single pollen record.

**Connell & Slatyer 1977. Mechanisms of succession in natural communities and their role in community stability and organization.**

Three models of succession, all of which agree that certain species appear first because they have evolved “colonizing” characteristics such as large no.’s of high-dispersal propagules, propagule dormancy, ability to germinate in unoccupied places, and rapid growth. In all models, early occupants modify the environment (via increasing shade and litter depth in forests, for example) so that it is unsuitable for further recruitment of early species; they must disappear. After establishment of the early successional species, the models differ as to what happens next:

1) Facilitation.

The early species modify the env. to favor later species. Sequence progresses until resident species no longer modifies the site in ways that facilitate the invasion and growth of a different species. Early species die via competition with later species.

Examples:

- primary succession (e.g. lichens on bare rock >> soil building)
- Saguaros recruit only under nurse plants of other species. (but might this be cyclic? it will be cyclic if saguaros don’t recruit under themselves)
- successions of scavengers on carcasses

Historically, Connell & Slatyer say, this sequence has been taken (by Clements, Odum) to show that communities are highly organized, highly integrated, organismal, and under “internal control.” They disagree. Presumably, they would argue that facilitation happens because of trade-offs: species that can do well in bare, low-nutrient sites cannot also be good competitors in richer sites.

2). Tolerance

Environmental modifications of early species neither increase or reduce the rates of recruitment and growth of later species. Site is increasingly dominated by “tolerant” species that can deal with the lower levels of resources on the site. Early species die via competition with later species.

Examples: Connell & Slatyer found “no convincing” ones

3) Inhibition

Early species hold resources and inhibit est. of later species; no species necessarily has competitive superiority over another (like ‘competitive equivalents’ of Hubbell 1997?). Later species cannot establish until earlier ones die off. They appear later because they live longer and so gradually accumulate as they replace earlier species. Early species die via disturbance or pests, not by competition with later species.

Examples:

Sutherland 1974: sedentary marine invertebrates hold space on tiles; other species invaded only after the original occupants died & sloughed off. (You would have to show that there is a difference betw. “early” and “late” species;

if any species can colonize and its chance, then all three of these models don't work).

**Connell 1971.** On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees.

Contrasts situations in which interspecific competition is mostly or entirely prevented (e.g. barnacles) with those in which competition is still important, but predators nonetheless keep competitive exclusion from happening (rainforest trees).

"... each tree species has host-specific enemies which attack it and any of its offspring which are close to the parent. The healthy parent tree supports a large population of these enemies without itself being killed, but the seedlings, whose growth is suppressed by heavy shade, succumb to the attack of insects and other enemies which come from the parent tree itself or the soil below it. A similar hypothesis, though differing in certain details, has been proposed independently by Janzen (1970)."

Connell states that his model differs from Janzen's in that Janzen talks about seed survival, where Connell talks about seedling and sapling survival. "However, we agree on the fundamental point that overall survival should be greater at greater distances from the parent." [Janzen in fact talks about seed and seedling survival].

Suggested mechanisms: 1) allelopathy ("much less likely") 2) intraspecific competition is more severe than interspecific b.c. of specialized nutrient requirements (rejected because main competition is for light, which isn't amenable to narrow niches) 2) attack by natural enemies is heaviest when species live in single-species aggregations. "For this mechanism to be effective the enemies must be both specialized in their choice of prey and not particularly mobile."

**Connell 1978.** Diversity in rain forests and coral reefs. *Science* 199:1302-1310.

**One sentence summary:** first elaboration of the intermediate disturbance hypothesis (IDH); beats up on equilibrium theories of species diversity (niche-diversification, circular networks, compensatory mortality) in favor of nonequilibrium ones (IDH, equal chance, gradual change). Evidence (both spatial and temporal) is given, but specific tests were not done.

Outlines proposed hypotheses of species diversity:

Nonequilibrium hypotheses

1. "Intermediate disturbance": diversity is higher when disturbance is intermediate in frequency and intensity. Evidence for frequency: successional sequences in tropical forests and coral reefs have highest diversity mid-succession. In early succession, few species are able to colonize; in late succession, competitive exclusion has had a chance to operate and weed out species, or (alternately) species resistant to enemies & physical extremes will hold most of the space. Monodominance is likely caused by absence of disturbance over long periods. Evidence for intensity: in tropical forests and coral reefs, large disturbances wipe everything out & must be completely recolonized by a small pool of colonization-adapted species, intermediate disturbances have two sources of species (regrowth from survivors, new colonists), and small disturbances are recolonized from the small number of spp. immediately surrounding the disturbance.
2. "Equal chance": species are competitively equivalent, so local diversity depends on regional species pool and local pop. density (this is called the "dispersal assembly" view today). Evidence for: Sale's work on tropical reef fish. Evidence against: Connell says that tropical forests are not likely to meet all the requirements of this model (equal offspring production and colonization probabilities, equal ability to resist physical extremes and natural enemies, equal competitive abilities).
3. "Gradual change": gradual environmental changes alter the ranking of competitive abilities, so that competitive exclusion never takes place & diversity remains high (originally proposed by Hutchinson for phytoplankton

assemblages).

Connell seems to think this is reasonable, but provides no evidence for or against.

#### Equilibrium hypotheses

1. "Niche diversification": each species is superior at exploiting a particular niche; high diversity results from a large number of subdivisions of the habitat. Species are "fitted in" with each other by natural selection. Connell says that both rainforest trees and corals are very generalized in their requirements, and the high species diversity in very small local areas argues against superfine niche partitioning.
2. "Circular networks": each species use interference mechanisms which cause it to win over some competitors but lose over others. A outcompetes B which outcompetes C which outcompetes A. Connell tested this idea on coral reefs and found no evidence for circular networks. Says it is untested for rainforests, but unlikely.
3. "Compensatory mortality": mortality falls heaviest on best competitors. Evidence for: a) the density- or frequency- dependent attacks on tropical tree seeds described in the Janzen/Connell (1970,1971) model b) in some corals, taller species that shade out others receive the most storm damage because they are stuck up where the water pushes them around most.

Evidence against: other tropical trees seeds/seedlings are not attacked in density-dependent fashion. Some top predators preferentially feed on rare species (e.g. starfish *Acanthaster*).

**Connell, J.H. (1970)** On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Proc. Adv. Study Inst. Dynamics Numbers Popul.* 298-312.

**One sentence summary:** Predation is a disturbance that can prevent competitive exclusion between prey species, and there are certain environmental situations in which this scenario can work.

Don labeled this paper as one on the "attenuation" of competitionism. It provides one mechanism in which tropical trees and marine invertebrates can avoid competitive exclusion. Predation is a disturbance which can reduce potentially competing prey populations to such low numbers that competition is diminished. Regarding the explanations for the maintenance of biological diversity, this theory is a type of "non-equilibrium" theory. Connell attempts to explain what conditions are required in natural ecological communities for this to happen. He uses two systems, barnacles and tropical trees.

He compares two sites with barnacles: Washington State and Scotland. In Scotland he finds that predators do not influence competitive exclusion as much as they do in Washington. He reasons that Scotland is a highly seasonal, un dependable , resource supply. There is a short, intense recruitment of barnacles because of weather fluctuations, which makes barnacle a rather inconsistent prey item. Due to the inconsistency of prey, it is costly to be a specialist, and no specialist predators are found. On the other hand, in Washington there are dependable resources, less weather fluctuations, and a longer period of larval recruitment. Barnacles as a prey item are consistent. One does find specialist predators because the food supply is consistent and they can keep up with the prey.

In tropical rainforest trees, one rarely finds stands of the same species of tree. Connell reasons that natural enemies may prevent competitive exclusion by preventing any one tree from forming a single species aggregation which could displace other species. The mechanism he suggests is that each tree species has host-specific enemies which attack it and any of its offspring which are close to the parent. The healthy parent tree can withstand the enemy attack, but the seedlings, suppressed by the shade of the adults, succumb to the attack. He shows that seed survival is best farther from the adult trees, and that attack by natural enemies is heaviest when trees live in single species aggregations. For this to succeed, the predators must be specialists, preferentially eating the dominant competitor.

Connell argues that predators are more vulnerable (shows some evidence) to weather fluctuations, and that a fluctuations can decrease the predator population such that it is not able to rebound quickly enough to control the prey. The prey then can compete strongly before the predator has an effect. Therefore, the sort of environment that allows this predator mediated behavior is one with few irregular occurrences of extreme weather, lower amplitude of variations in temperature, rainfall, etc. In such places enemies should be more specialized. There would be less of a

chance for prey to increase suddenly beyond control of predators since unfavorable seasons are reduced in length and severity.

**Connor, R. C.** 1995. The benefits of mutualism: a conceptual framework. *Biological Reviews* 70:427-457.

Previous taxonomies of mutualisms (e.g. dividing along the axes of facultative vs. obligate, diffuse vs. one-to-one, transient vs. permanent; or Janzen's functional classification into harvest mutualisms, pollination, seed dispersal, etc.) are unsatisfactory because they do not describe the mechanisms by which organisms interact [or "trade" in Schwartz's terminology.]. A new classification is proposed that divides the mechanisms of obtaining benefits from the partner into 3 categories:

1. by-product benefits are those which come at no cost to the partner & result from his normal activities.
2. invested benefits are those which accrue via investment in the partner which gives fitness returns greater than the original investment purloined
3. benefits are those taken via predation or parasitism (for this to be part of a mutualism, the indiv. being purloined must receive by-product or invested benefits that exceed the cost of being purloined). [How can you tell if organism A is purloining from B or if B is actively investing in A? fallacy of intent]

These 3 mechanisms can be combined into 6 "basal mutualisms" which describe the potential range of starting points. From these basal mutualisms, the interactions can evolve (i.e. a partner that provides by-products can change to one that invests) and the original currencies can be obscured.

examples:

- 1) by-product, by-product: mixed species flocks
- 2) by-product, purloined: cowbird-oropendola (cowbird steals food, host gets by-product of cowbird removing botfly larvae from chicks)
- 3) invested, purloined: damselfish-algal lawns (damselfish predares on alga, alga gets investment of being 'farmed' - damselfish removes competing algae)
- 4) invested, invested: ant-acacia

The Prisoner's dilemma in many (most?) cases may not be the most parsimonious explanation for mutualism. In many cases (eg lycaenid-ant interaction in which ants protect caterpillar which secretes food), the payoff for cooperation exceeds the payoff for defection ( $R > T$ ) and the rules of the game are violated. The emphasis by Axelrod and others on the Prisoner's dilemma and TIT FOR TAT comes from an ignorance of by-product benefits which can get mutualisms started.

**Cornell, H. V.** 1993. Unsaturated Patterns in Species Assemblages: The Role of Regional Processes in Setting Local Species Richness. In Ricklefs & Schluter, *Species Diversity in Ecological Communities*.

**One sentence summary:** Theory does not predict whether communities should be saturated, while more field work is needed to determine generalizations. Historical / phylogenetic effects may be key to the community structure implying community ecology is a historical science.

1. Theoretical Communities:

- a) Interactive: Biotic interactions among community members.
  - i) Niche Heterogeneity Models
    - Coexistence favored by differences in niche dimensions
    - All models predict saturation
    - examples: MacArthur, 72; Tilman 85; Chesson & Huntly, 89.
  - ii) Spatio-Temporal Heterogeneity Models
    - a) Four methods of coexistence
      - (1) Competitive equivalents with unpredictable recruitment due to

- disturbance - Lottery and Random Walk models
  - (a) No Saturation
- (2) Aggregated utilization of fragmented resources
  - (a) Saturation
- (3) Periodic disturbance with slow population growth
  - (a) Saturation
- (4) Spatial variation on specialist predation of new recruits
  - (a) No Saturation
- b) NonInteractive
  - i) Density independent fluctuations in abiotic environment
  - ii) Source / Sink communities
    - a) Exist in extreme environments / edge of range
  - iii) Caswell's Model I
    - a) Pure non-interaction
    - b) Identical species response to abiotic factors
    - c) No saturation (infinite niches)
- 2. Real Communities:
  - a) Proportional richness
    - i) Linear relationship between regional and local richness
  - b) Saturation ("ceiling")
    - i) asymptotic (non-linear) relationship between regional and local richness
  - c) Empirical studies support only proportional richness or are ambiguous.
  - d) Due to evolutionary scale factors, regional diversity is independent of local diversity
  - e) Historical differences in proliferation of taxa can effect guild structure. These effects directly influence regional diversity. Diversification may set regional richness by host shifting or by cospeciation.

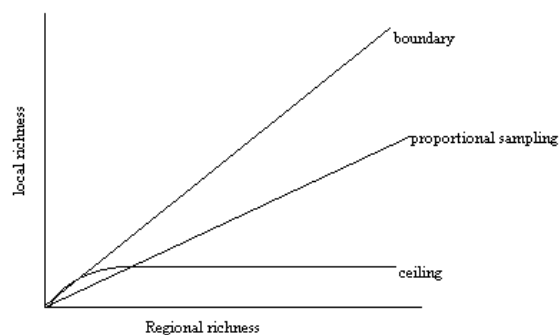
**Cornell, H.V.** 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. In *Species diversity in ecological communities: historical and geographical perspectives*. Ricklefs, R.E. & Schluter, D. (eds). Pages 243-252. U of C Press.

The question: are communities saturated with species?

Saturation: there is an upper limit to local richness that is independent of the size of the regional colonization pool in the sense that further increases in regional richness will have little influence on local richness.

Some theories about the structure of ecological communities, e.g., niche, resource ratio. predict saturation, while others don't, e.g. the lottery model, random walk.

Theoretical relationships between local and regional richness:



## Community Ecology Literature Review

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Comparative method: compare local and regional species richness to see if community saturated.

Most empirical work suggests that patterns reflect proportional sampling.

Chicken or egg problem: whether local richness derives mainly from broad-scale processes underlying regional richness or vice versa.

Observation: communities are generally more unsaturated than saturated, so the direction of richness control should be from regional to local, not vice versa.

The generation of regional richness in evolutionary time may not just reflect local ecology but also heavily influenced by phylogenetic history.

“The tendency to proliferate may be an intrinsic historical property of specific taxa, based on their genetic and biogeographical attributes, and may be effectively independent of niche complexity and local ecology. Local ecological opportunity may thus have little impact on regional richness, and ultimately, on richness levels in local assemblages, over both ecological and evolutionary time.”

Example: diversification of phytophagous insect species assemblages (guild structure)

**Darnell, R.M. 1961.** Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology* 42: 553-568.

**The main point:** there is no such thing as distinct trophic levels. Rather, what animals eat is better represented by a trophic spectrum which incorporates omnivory, nutritional opportunism, ontogenetic changes and the importance of the complicated role of detritus. Argument against aquatic trophic cascades.

**Methods and Results:** looked at stomach contents of the 35 most important consumers living in this lake in an attempt to related consumer nutrition to primary production and interpret those results in the context of the entire community. Found that consumers ate all sorts of things. In fact, the paper is essentially a long exposition of the variety of food items consumed! They interpret consumers' ability to eat a variety of foods as evidence that consumers buffer the community against destabilization.

**Trophic spectrum:** construct a table as follows: represent all food categories on the left and list the species across the top row. Use horizontal bands whose height corresponds to the relative percent eaten for that species. This is better drawn: (the figure from the paper is also duplicated in Don's notes)

FOOD TYPE	SPECIES 1	SPECIES 2
FOOD TYPE I		
FOOD TYPE II		
FOOD TYPE III		

**Dayton, P. K. 1972.** Competition, Disturbance and community organization: The provision and subsequent utilization of space in rocky intertidal community. *Ecological Monographs*. V41(4):351-389

**One sentence summary:** In rocky intertidal communities the competition model is not strongly supported as disturbance plays at least as large a role in determining community structure.

In rocky intertidal communities space is the key limiting resource. The populations of invertebrates and algae all compete for space. While it is clear that *Mytilus californianus* (a mussel) is the dominant competitor, the other populations exist in substantial numbers.

The research focused around a set of experiments that were designed to determine the relationship between disturbance and effect on populations. The experiments conducted created exclusion zones with manipulated species diversities. Populations are maintained by disturbances:

Abiotic Forces:

Wave Exposure	Controls algae
Log Battering	Controls <i>M. californianus</i>
Desiccation	Controls algae and anemone

Biotic Forces:

Limpets	Affect algae and barnacle recruitment
Gastropods	Affect barnacles
Asteroids	Eat mussels

Thus in rocky intertidal communities, the competitive model of communities is not strongly supported. Continuous disturbance with complex food web dynamics confound simple competition for space. This is posited as the reason for the existence of multiple species.

**Dennis, B., and Taper, M. L., 1994.** Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* 64(2):205-24.

**One sentence summary:** Statistical density dependence does not necessarily indicate ecological density dependence, at least not in any simple way.

Dennis and Taper, 1994 (DT) is part of a literature that has been accumulating since 1960 at least on using statistical analyses to estimate the prevalence of density-dependent regulation (DDR) of population size, where DDR means that population growth is in some sense a function of population size. In this literature, the basic units of discourse are time series, meaning sequences of population sizes observed at regular intervals, and tests for density dependence, meaning procedures for computing a test statistic from a time series, comparing it with a critical value, and accordingly either retaining a null hypothesis meant to signify the absence of density dependence or accepting an alternate hypothesis meant to signify the presence of density dependence. On the face of it, DT belongs to the established tradition of articles that call attention to shortcomings of older tests, present new ones, and investigate their properties. To be sure, it does all this with outstanding clarity and thoroughness. However, its discussion of the interpretation of test results transcends this tradition. DT challenges conventional perspectives on density dependence testing by contending that a positive result of a density dependence test should be firmly distinguished from a demonstration of DDR. A positive test result means that an additional parameter in the model underlying the test yields an improvement in the description of the data by the model that is significant in a statistically specified sense; generally, it is permissible to interpret this as indicating a return tendency in the data: small populations tend to grow, and large populations tend to shrink. If DDR is operating, then positive test results are expected most of the time. However, any stochastic process with a stationary distribution typically gives data that test positive, and such a process need not be an instance of DDR, at least not in any simple way. Thus caution is in order when interpreting positive results of density dependence tests. As DT says, "We believe [our] test can be a useful component of a case for ecological density dependence, but should not be the sole component." (p. 222)

By the way, the main point is nicely elaborated in Wolda and Dennis, 1993 (Density dependence tests, are they?, *Oecologia* 95:581-91), which applies the test developed in DT to a large assortment of observed time series, finding statistical density dependence in a number of contexts where it is unreasonable to attribute ecological density dependence, e.g., island populations of moths regenerated from scratch annually by immigrants from a mainland population.

**Ehrlich, P.R. & Raven, P.H. (1964)** Butterflies and Plants: A study in coevolution.

**One sentence summary:** First theory of biochemical coevolution, in which the synthesis of secondary compounds as plant toxins is specifically related to patterns of host plant utilization by phytophagous insects. Stepwise reciprocal selective response.

Summary:

Examines relationship between butterflies and their food plants to answer questions about community evolution. Factors determining food choice of Lepidoptera include: geographical and ecological range considerations, choice of oviposition, larval choice, structural and mechanical plant characteristics, and chemical factors. Compiled literature and knowledge of taxonomists to establish food plants of butterflies (NOTE: the paper talks about 5 families of butterflies and their subfamilies. Patterns deal with large patterns of family and subfamily associations with certain families of plants. Today, some of these subfamilies have been elevated to family status,

and there are 10 families. I do not know what kind of difference this makes with the phylogenetic aspects of this paper, but it is worthy noting.) Choices exercised by phytophagous organisms may provide approximate, but nevertheless useful indications of biochemical similarities among groups of plants. Do not necessarily indicate the plants' overall phenetic or phylogenetic relationship. Examining patterns found that diversification of butterflies has been elaborated against a dicotyledonous background. Appearance of dicotyledons predated appearance of butterflies, and switches to other groups of plants such as gymnosperms or monocots would be derived (don't know if this still holds). Records of food plants shows constant relationships: plants usually fed upon by a single, phenetically coherent group of butterflies or several closely related groups. Secondary plant substances play the leading role in determining patterns of utilization by phytophagous insects. Sounds like this is the first paper that explained why secondary compounds might exist in angiosperms.

Idea of coevolutionary arms race:

Through mutation or recombination, plant develops repellent substance and is protected from attacks of phytophagous animals. This would allow it to enter a new adaptive zone. Evolutionary radiation of the plants follows and what was a chance mutation might characterize an entire family or group of related plants. Insects can evolve in response to physiological obstacles (evidenced by pesticide resistance) and mutation might appear that allowed it to feed on the previously protected plant. Selection could carry the line into a new adaptive zone. Group free to diversify largely in absence of competition. Diversity of plants not only may tend to augment the diversity of phytophagous insects, the converse may also be true. After restriction to a formerly repellent substance, that substance may evolve to be an attractant. Coevolution may carry to higher trophic levels also.

Interesting conclusions:

Secondary compounds may explain how angiosperms diversified from gymnosperms.

May explain latitudinal gradient, which seems a haphazard thing to toss in at the end, and not very mechanistic.

#### **Erlich & Birch 1967. The "balance of nature" and "population control."**

Criticizes HSS as taking a naive balance of nature approach and thus getting it wrong. We should not expect generalizations to hold up; instead, each population is undergoing all kinds of fluctuations. Populations sizes result from stochastic rather than deterministic processes, and talking about the trophic level as a whole is silly. "One of the most common fallacies in population biology": that persistence of a species implies population control.

Take issue with HSS observation no. 1, that herbivores do not commonly control plant populations. Erlich & Birch make the point that we wouldn't necessarily see it; e.g. if you went to Australia today & saw how few *Opuntia* there are, you wouldn't know it was because of *Cactoblastis* moth even though they limit the cactus pops.

A central problem with HSS is that "food-limited" doesn't really mean anything.

Another is that HSS incorrectly draws conclusions about populations from reasoning about trophic levels (assume trophic levels mean something for the moment). Decomposer example: if species A dominates during the wet part of the year, but then dies out during the dry period and lets B dominate, both are abiotically limited even though all energy in detritus is processed and HSS would call the decomposer level "food-limited".

DRS says this paper shows that "relative [food] shortage is more important in pop. regulation [than absolute?]" but I can find no mention of this topic.

#### **Erlich & Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586-608.**

**One sentence summary:** According to Kingsolver & Paine, this is the "first systematic exploration of the evolutionary consequences of ecological interactions across trophic levels"; previous approaches (Lack, Harper,

Hutchinson) had focused on single species or sets of competing species. (First?) definition of coevolution. “The coevolutionary ‘arms race’ represents a much more dynamical view of the evolution of community diversity than Hutchinson (1959) and MacArthur (1958), in which the number of coexisting competitors is strictly limited by the volume of available niche space.”

The first third of the paper consists of a discussion of what butterfly genera eat what plant families [I can’t believe they didn’t put it in table form in an appendix]. This is the basis for the generalization that “plant [groups] are fed upon by a single, phenetically coherent group of butterflies or several closely related groups.” The effects of secondary chemicals on restricting butterfly use are discussed; “...secondary plant substances play the leading role in determining patterns of utilization.”

The coevolutionary process is then elaborated. A plant possessing a defensive compound “would in a sense have entered a new adaptive zone. Evolutionary radiation might follow, and eventually what began as a chance mutation or recombination might characterize an entire family or group of related families.... [the same mutational process might happen to an insect population] carry[ing] the line into a new adaptive zone. Here it would be free to diversify largely in the absence of competition from other phytophagous animals.” Specialization of insects would be enforced via physiological or predation costs of switching to a new host plant. Repellents might become attractants.

No mechanism is given for speciation (is speciation even mentioned?) or adaptive radiation. In summary, they hypothesize that “plants and phytophagous insects have evolved in part in response to one another...in a stepwise manner.” It is suggested that this mechanism may be responsible for high tropical diversity: “the rich diversity of tropical communities may be traced in large part to the hospitality of warm climates toward poikilothermal phytophagous insects.”

**Estes, J.A. & Palmisano, J.F.** 1974. Sea otters: their role in structuring nearshore communities. *Science* 185: 1058-1060.

**The main point:** sea otters may act as keystone species by reducing herbivore density, thereby causing producers to proliferate. Support for HSS? A real example of an aquatic trophic cascade?

**The system:** sea otters ← herbivores (sea urchins) ← macrophytes (kelp)

**Methods and Results:** compared two Aleutian islands: 1. one island had been extensively hunted for sea otters in the 18th century and the sea otter population never recovered. The intertidal community had been completely grazed over by big fat urchins and was marked by extensive mussel beds and dense barnacles; 2. the other island had also been hunted but otter density has since been restored. This island had an “almost complete mat of ... kelp”

**Their summary:** “the otters effectively control sea urchin populations, and the absence of grazing pressure allow vegetational communities to flourish.”

**Don's take:** kelp-urchin-otter aquatic trophic cascade as “vignette”

**Farrell** 1991. Models and mechanisms of succession: an example from a rocky intertidal community

Oregon coast. Experimental clearing of patches to determine sequence of succession, and then removal experiments to determine mechanisms. Succession always occurred in same sequence of spp. coming & going, but rates differed 3-fold.

*Chthamalus* barnacle is first colonist; is gradually competitively excluded by *Balanus* barnacle. 3 spp. macroalgae can only colonize after *Balanus* establishes (grow as epibionts on tests of barnacle). Algae create more drag & set up patch to be cleared by wave action.

Mechanisms: *Chthamalus* does not affect establishment of *Balanus* (tolerance model), but is competitively excluded by it. *Balanus* facilitates algal recruitment by decreasing limpet grazing rates (I guess limpets can clean the rock surface but can’t climb up on barnacles?). Consumers (limpets) slowed succession by delaying *Balanus* est., and by delaying algae est. However this is not considered inhibition because limpets are not “basal (sessile)” species, and the C&S models refer only to these basal species.

Important point: a single Connell-Slatyer type of model did not apply to the succession; the barnacle interaction

follows the tolerance model, while the barnacle-algae interaction follows facilitation. [This is similar to the Walker & Chapin observation that a mixture of model elements is needed to explain Alaskan alder → spruce succession]

**Feeny, P.** Plant apparency and chemical defense. In *Recent Advances in Phytochemistry*. pp 1-40

Note: Terminology is Feeny's own.

**One sentence summary:** There is an association to the type of chemical defense a plant exhibits (termed quantitative and qualitative) and its apparency (a fancy term for different life history strategies).

**Two types of chemical defenses:**

- 1) qualitative-effective even in small concentrations against non-adaptive insects, but evidently susceptible to rapid detoxification by adapted insects. When countered by specific adaptation have little effect on the variable (phenotypic) cost of insect growth. Example-glucosinolates in crucifers.
- 2) quantitative-dosage dependent (greater the concentration, greater the inhibition of larval growth) even to insects which naturally feed on leaves containing them. By increasing variable cost of growth, reduce growth rates and hence fitness of wide range of insects which eat them.

**Definition of apparency and examples:**

- 1) unapparent-e.g. crucifers, early successional species, "hard to find" by their adapted enemies and escape primarily in time and space. Can't afford metabolic cost of high concentrations of defenses because it's likely to reduce metabolic allocation for growth and reproduction on which these types of species depend
- 2) apparent-e.g. oaks, climax dominants, "bound to be found" by enemies in ecological time. Predation on undefended plants likely to be severe. Allocation to defense likely to increase fitness. Apparency refers to these plants' visibility, conspicuousness in whatever means to herbivores.

**Hypotheses** of paper (Note importance of effects of adapted vs. non-adapted enemies), greater part of this paper is spent explaining empirical and anecdotal examples that support these hypotheses:

1. The proportion of metabolic resources allocated to chemical defense tends to be greater in plant species which are characteristically apparent than in characteristically unapparent species, at least within the same biome. The greater the apparency of a plant species, the greater the concentration of defensive compounds likely to be present in its tissues.
2. The qualitative nature of defensive compounds present in plants changes along a gradient of species apparency between the following extremes:
  - a) Unapparent plants contain compounds which are effective in relatively small concentrations as toxins against non-adapted enemies, for which they may serve also as behavioral deterrents. Such compounds are likely to be susceptible to counter-adaptation, however, and may have little inhibitory effect on the growth and fitness of adapted enemies, which may exploit them as attractants or feeding stimulants.
  - b) Apparent plants contain compounds which are not readily susceptible to counter-adaptation and which serve to reduce the growth rate and fitness of all enemies, even though relatively high concentrations may be required to be effective. such chemical defense is generally associated with low nutritive value for herbivores and pathogens, and with relatively tough leaves.
3. The chemical defenses of the component parts (leaves, roots, etc.) of a plant vary both among such parts and also through an generation time as a function of their varying component apparencies to different arrays of enemies, and as a function of varying component importance to plant fitness.
4. Within any one biome, at least, interspecific diversity of defensive compounds is lower in communities characterized by apparent plants than in those typified by unapparent species.

**Interesting Conclusions:**

1. patterns of chemicals in plants may have profound effects on the life histories of insects. early successional (unapparent) plants may impose ephemeral "r-selected" life histories on their associated insects and similarly for apparent plants-they may impose K-selected patterns on their insect herbivores by imposing slow growth on them.
2. Current agricultural practices make commonly unapparent plants apparent. Increase in herbivores means increase in pesticides. Based on the hypotheses of this paper there is a benefit to be gained from crop rotation

and diversiculture which would limit the plants' apparency.

**Flenley 1993.** The origins of diversity in tropical rain forests. *TREE* 8:119-120.

**One sentence summary:** refugia hypothesis (refugia as "species pump") not supported for C. America.

A 1-pager describing Bush et al.'s (1993) analysis of a pollen core from a 650m elev. lake in Panama. Under the refugia hypothesis, this site should have been a refugia for lowland species during the Pleistocene. Instead the pollen record show that it was occupied by cool-adapted, lower-montane species and thus could not have supported the lowland species. Does not falsify the hypothesis, but requires that the presumed refugia be located somewhere else.

**Freeman, S., and Rodriguez, R. J., 1993.** Genetic conversion of a fungal plant pathogen to a nonpathogenic, endophytic mutualist. *Science* 260:75-8.

**One-sentence summary:** One mutation may make the difference between a parasite and a mutualist.

This is a charming tale of a reformed parasite. The fungus *Colletotrichum magna* attacks many plants, including "the majority of agricultural crops grown worldwide" (p. 76), first penetrating (typically) the roots and then growing through the plant, killing the plant as it grows. The authors report a mutant strain, designated path-1, which they have shown has three interesting properties:

- (1) In the host plants tested, path-1 penetrates and grows but does not damage the plant appreciably. It grows slower than the wild type, and it was unknown in 1993 whether it like the wild type grows into fruits, but its host plant compatibility appears identical to that of the wild type.
- (2) Plants inoculated with path-1 are highly resistant not only to wild-type *C. magna* but also to at least one other fungal pathogen---in this sense, path-1 is a mutualist. It seems that path-1 somehow primes host plant defenses, but the mechanism was unknown in 1993.
- (3) Crosses of path-1 and another strain suggest that a single locus is mutated in path-1. Thus one mutation may make the difference between a parasite and a mutualist.

**Frellich et al. 1993.** Patch formation and maintenance in an old-growth hemlock-hardwood forest

Michigan wilderness area in which hemlock and sugar maple dominate different patches, and occur in mixed stands as well. Spatial autocorrelation analysis was used to determine associations between over-and under-story trees. Hemlock and sugar maple had a strongly negative reciprocal association (subadults of one NOT likely found underneath other), and each one had a strong positive association with itself; thus no reciprocal replacement type of succession is going on, and monodominant patches result. Suggested mechanisms (not tested): thick litter under sugar maples inhibits hemlock establishment, and low N under hemlock likely inhibits maples. In contrast, sugar maple and yellow birch have a neutral association and form mixed stands.

Four hypotheses tested for patch formation:

- 1) Soils and topography: can explain Red Maple domination of the swamp part of the plot, but not the division between the Sugar Maple and Hemlock patches (either of which could dominate the whole upland part of the plot in the absence of the other).
- 2) Disturbance history: no evidence of wind or fire damage in past 150 years.
- 3) Competitive interaction hypothesis:
  - a) negative reciprocal association: leads to monodominant patches
  - b) positive reciprocal association: leads to mixed stands
  - c) neutral association: leads to mixed stands
  - d) one-way association (one species has a greater + or - effect on the second species than the second species does on itself): leads to successional replacement & loss of one species
- 4) Pattern of invasion hypothesis: hemlock arrived in this system only 3000 yrs ago, so existing patch structure might reflect pattern of invasion. Probably invaded uplands after initial est. in high-moisture areas next to bogs.

Thus 3a & 4 are the best explanation of patches in this system. Simulation models using these assumptions were able to replicate patchy structure after 3000 yrs, whether started with equal parts maple/hemlock or small no.'s of hemlock invading maple stands. That hemlock numbers increase indicate that it, as the better competitor, eventually will expand its patches to the point where maple disappears.

**Gaines & Bertness 1992.** Dispersal of juveniles and variable recruitment is sessile marine species.

Implications for succession: history can play an important role because of the high variability in what species arrive at a site, and in what numbers.

Variable dispersal is a major source of recruitment variation in a Narragansett Bay barnacle (and by extension, many sessile marine animals with planktonic larvae). Recruitment (individuals/m<sup>2</sup>/year) increases linearly with decreasing flushing rates of the bay. This may explain why studies of reproductive output by adults and juvenile mortality have not been sufficient to explain the high variability in recruitment.

**Gaines, S. & Roughgarden, J.** 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *PNAS* 82: 3707-3711.

**One sentence summary:** differences in settlement rate can account for differences in population structure.

The system: barnacles in the intertidal. Two populations: one with high settlement rate, the other with low settlement rate.

Methods: photographed via automatic camera (!) the seasonal and yearly changes in abundance of barnacles in the two populations over three years. Settlement rate is directly proportional to the amount of unoccupied space.

Results:

Low settlement rate population: large yearly differences in average free space (between year differences > within year differences). Yearly differences reflect the differences in rate of settlement for each year. Low average abundance.

High settlement rate population: no significant differences in average free space between years, but large differences within years. These within-year differences are significantly oscillatory. High average abundance.

Density-dependent mortality rates are nearly identical for the two populations, so spatial variation in mortality after settlement cannot cause the observed spatial variation.

Conclusion: settlement rate seems to play as important a role as post settlement processes, e.g. predation and competition.

**Goldberg, D. E.** 1990. Components of resource competition in plant communities. In *Perspectives on Plant Competition*, pp. 27-49. Academic Press.

Brief summary: Goldberg is interested in when competition will happen, rather than its outcome. This requires a new framework in which competition is viewed as an indirect interaction mediated by an intermediary (e.g., resources, herbivores, symbionts). Plants interact with the intermediary in two distinct ways: via effects on and responses to the abundance of the intermediary. Only when the effects and responses are nonzero and of opposite sign is competition possible. For example, when plants deplete a particular resource ( - effect) which contributes to growth (+ response), competition is possible. Plants can be good competitors either by being good extractors (effect pathway) or good tolerators (response pathway).

For resources, plants exert their effects via 2 classes of mechanisms:

uptake and non-uptake. Uptake always results in (-) effects and is the focus of most studies, but non-uptake mechanisms can result in (+) as well as (-) effects (e.g., litterfall can increase soil nutrients, shading can increase soil moisture retention). Non-uptake mechanisms are generally not included in competition models, even those that

explicitly include resources.

Effect on and response to resources can be decoupled; not recognizing this fact may lead to erroneous conclusions about when competition is, or is not, occurring. For example, for *Ambrosia* shrubs and *Plantago* herbs growing in Michigan oldfields, the herb shows a significant positive response to water addition, suggesting that the shrubs are competitively suppressing the herbs. However, the shrub did not significantly change soil moisture; increased extraction was balanced by increased shading which decreased evaporation from the soil surface. Similarly, the shrub decreased available light, but the herb did not show a response to reduced light. Thus a situation with no net competitive effects could have looked like competition.

Predictions:

- 1) species that have large (-) effects on resources are likely to be dominant in communities where persistence is determined by size-symmetric competition (e.g., early succession, gaps).
- 2) species that tolerate low resources levels (modified response) will be dominant where persistence is determined by size-asymmetric competition (e.g. seedlings recruiting under mature vegetation).
- 3) competition for light will be strongest at the high-productivity end of the productivity gradient (increased standing crop decreases light penetration, and there is no mechanism by which plants can have a (+) effect on light)
- 4) competition for soil resources will be weakest at the low-productivity end, since there is more room for (+) effects (e.g., organic matter accumulation under desert shrubs facilitates growth of annuals).

**Grubb, P.J.** 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52: 107-145.

**One sentence summary:** Differences in requirements for regeneration (the regeneration niche) may be more important than habitat niche partitioning for maintaining species diversity.

What maintains plant diversity? Grubb starts with this list:

- Variation in life form
- Phenological spread (seasonality)
- Environmental heterogeneity
- Positive interactions (mutualism)
- Variation in competitive ability with age

But what about how plant species differ in the likelihood that they might replace a dead plant? This is the Regeneration niche. Plants differ with respect to

- Seed production
- Dispersal in space and time
- Germination
- Establishment of seedlings
- Seedling to adult phase

Differences between species with respect to these factors may determine who replaces a dead plant ( these differences may maintain diversity because one species will not always be the most able/available to replace the plant.

**Haffer, J.** 1969. Speciation in Amazonian forest birds. *Science* 165(3889): 131-137.

**One-sentence summary:** “Species pump” hypothesis: Amazonian forest patches shrink and get isolated when it gets dry, allowing for allopatric speciation, and then grow and merge back together when the climate gets wetter. Repeat several times and you have high tropical diversity. A nice idea at the time, but evidence since then hasn’t supported it.

Slightly longer summary: Repeated isolation and reunification of forest “refugia” as the climate alternately dried and

became wetter during the Pleistocene era is proposed as a mechanism for repeated allopatric speciation of birds in the Amazon basin. An intellectually sound hypothesis given the state of knowledge at the time, but the evidence for it isn't very strong and I am not sure that the same principles can be applied broadly to explain species diversity in other taxa and locations. It does remind us of the importance of historical occurrences in determining community structure.

In this paper, Haffer hypothesizes a mechanism for the production of high diversity among birds of the Amazonian rain forest. He hypothesizes that climatic cycles during the Pleistocene and post-Pleistocene alternately separated and rejoined patches of forest. During the dry periods when forest refugia were separated, allopatric speciation occurred. Studies of pollen cores in northern South America apparently indicate repeated climatic cycling, and evidence exists indicating a high rate of evolutionary change in bird fauna during the Pleistocene. Haffer predicts the location of refugia based on: 1) current rainfall data (the assumption here is that areas of present-day rainfall maxima remained wet enough to support forest even during the dry periods), and 2) current distributions of localized forms apparently derived from a common ancestor. Nine probable refugia are listed and several smaller ones are postulated based on this information. Haffer uses an estimate that the time required for speciation is on the order of 10,000 or 100,000 years, and concludes based on this that speciation could have occurred repeatedly during the Quaternary.

It is a provocative theory which makes some interesting predictions, though the evidence which Haffer uses is somewhat weak. There is no palynological evidence that forest fragments became disconnected from one another during the climatic fluctuations, though that certainly is possible. However, this paper certainly does put forward an interesting, testable hypothesis. Its main weakness is the sheer lack of pollen core and climatic data necessary to confirm it.

Eventually this hypothesis ended up in the dust bin of history: distributions of present-day Amazonian organisms should all suggest the same locations for refugia, and they don't. However, Haffer is right in reminding us that idiosyncratic historical events can play a very important role in determining community composition and diversity.

**Hairston & Hairston 1997.** Does food-web complexity eliminate trophic-level dynamics? *Am Nat* 149:1001-1007.

A reply to Polis & Stong 1996. While they agree that the complexities that P&S outline could potentially "lead to a negation of general [food web] patterns," they disagree that the "mere existence of such complexity necessitates a rejection of general patterns." Trophic levels do exist. Point out that P&S have done no experimental manipulations of the webs they describe.

General patterns do exist: in aquatic systems, secondary carnivores hold down the primary carnivores and allow algae to be depressed by the zooplankton. In terrestrial systems, secondary carnivores are unimportant, and primary carnivores are ineffective at suppressing herbivores leading to less herbivory. H&H claim that these patterns explain the fact that consumption efficiency (% of primary productivity eaten) is much higher in freshwater pelagic communities (32%) than in terrestrial communities (3%).

ATC's: H&H disagree with statement that algae are not well-defended. Disagree that the "edibility" of algae is the reason why trophic cascades (TC's) are found in aquatic sys. Instead, the fact that the aquatic primary carnivore and secondary carnivore trophic levels "are dominated by a few species of relatively easily manipulated animals" contained within natural boundaries (lake edge) explain why we can force TC's in water. Also, aquatic plants and herbivores have short generation times & can show a rapid response to manipulation. We don't see TC's on land because organisms are longer-lived and carnivores are more diverse & resistant to removal, not because TTC's don't exist.

Evidence for terrestrial trophic cascades:

Spiller and Schoener (1988, 1990): lizards and spiders are the dominant predators of herbivorous insects on Staniel Cay, Bahamas. Removal of them leads to increases in homopterans and midges and decreases in plant biomass.

[The P&S vs. H&H debate reminds me of ancient ecology, where people had massive wars that basically got down to semantics; one group thinks A is more important than B, while the other thinks B is more important than A; but what does "important" really mean? A lack of testable hypotheses. P&S think that top-down control is not pervasive in nature, H&H think it is; but the only way to answer this debate is to catalog all the webs in nature, experimentally manipulate them, and vote-count. Instead, both sides amass anecdotal evidence.]

**Hairston, N. G. Jr. & N. G. Hairston Sr.** 1993. Cause-effect relationships in energy flow, trophic structure and interspecific interactions. *Am Nat.* 142: 379-411.

**One sentence summary:** A comparison of two concepts: 1) The number of levels of a trophic structure are governed by the amount of energy that transferred at each level 2) The trophic structure is controlled by the interactions (competition and predation) with competition controlling detritivores, producers and carnivores with predation controlling herbivores - HSS. It is no surprise, based on the authors, that 2) is the favored concept.

The focus is on three systems - forests, grasslands, and freshwater lakes. They express concern about the fluid definitions of food webs and trophic levels. Their solution is to ignore structure that is not suited to the conclusion that HSS is the valid format. Their definitions, when given, appear not to add clarity to already muddied waters.

Trophic level: "a group of organisms acquiring a considerable majority of its energy from the adjacent level nearer the abiotic source." This definition is not satisfactory when considering the age structured food consumption of species. Considerable majority is not defined.

They claim that omnivory limits the number of trophic levels without clearly defining the location of an omnivore in the trophic structure (by the definition of trophic level, there really are no omnivores, as the majority energy source is considered for placing an organism in a trophic level). The placement of organisms in trophic levels is discussed with the notable concept that they place granivores, nectivores and pollen feeders in the carnivore trophic level [gee, bees and butterflies as carnivores??]. Omnivory is discounted as a confounding factor in trophic levels by sifting reviews of anecdotal evidence.

The discussion of trophic levels revolves around terms like "reasonably distinct", "moderately well-defined" and "largely consistent" with much discussion about the structural dependence on the specific organisms in the ecosystem. They conclude that pelagic systems have four levels and terrestrial three. From this they claim testable hypotheses exit.

The rest of the paper is a review of studies of different systems that result in the generation of energy flow diagrams. The authors caveat that the studies have poor statistics (including evidence that more than 100% of the primary production is consumed), but this does not deter them. Finally they conclude that energy flow is controlled by the trophic structure and this is all dependent on the specific relationships of the organisms.

**Hairston, N.G., F.E. Smith, and L.B. Slobodkin.(HSS)** (1960) Community structure, population control, and competition. *Amer. Nat.* 94:421-425.

**One sentence summary:** The world is green, so herbivores don't eat all the plants which means predators control herbivores.

This is a seminal paper, as we all know. It asserts that plant diversity is a result of carnivores, an idea that is both controversial and ambiguous. Don uses it with regard to two phenomena: diversity and food webs. With regard to diversity, HSS says that carnivores can suppress herbivores and thus release plants to flourish and compete. This assumes that if herbivores were not kept in check, plant diversity would diminish because herbivores would eat all the plants. That is the mechanism (rather flimsy) that Don places this under to explain the maintenance of species diversity.

Don outlined well the importance of this paper in food web theory. I will briefly reiterate these points here. The key hypothesis that everyone argues with is that by suppressing herbivore populations, plants thereby protect plant populations. This is reasoned by the following sequence. Fossil fuels are not now accumulating, so all energy flows through the biosphere (not true-DRS). All organisms limited by the amount of energy fixed( kind of true, false

because of detritus). Decomposers remain food limited. Any population not resource limited is limited below the resource limit. Catastrophes are exceptional. Because producers are neither herbivore nor catastrophe limited, they must be limited by their own exhaustion of resources (key assumption). Temporary exceptions to depletion of plants by herbivores occur, so herbivores are not usually limited by their food supply. By elimination, predation and parasitism are the only viable remaining means of control of herbivores. Because predators and parasites limit their own resources, as a group they must be food limited. Territoriality of predators cannot generally be important because if it were, herbivore populations would increase and deplete vegetation. Decomposers, producers, and predators are resource limited.

**Hairston, Smith, Slobodkin 1960. Community structure, population control, and competition.**

Addresses the problem of population regulation through deductive reasoning. Populations in different trophic levels are expected to differ in their methods of control. Base argument: since rate of accumulation of fossil fuels is negligible (DRS says this has been shown to be untrue), all the energy fixed by photosynthesis flows through the biosphere; thus "all organisms taken together are limited by the amount of energy fixed." [If they weren't, they would exist below their max levels, and there would be leftover energy to form fossil fuels].

Observations:

1. herbivores do not commonly deplete plants
2. catastrophes do not commonly deplete plants
3. temporary exceptions to #1 are caused when herbivores are protected (e.g. introductions) - thus herbivores are not usu. food-limited & we must look for another mechanism

PREDATION is the mechanism [Interesting little community-level selection argument: if a plant community allowed itself to be killed by grazing, another one would take its place; thus the most "persistent" communities are those in which predators "hold down" the numbers of herbivores]

Conclusions:

- "1) Populations of producers, carnivores, and decomposers are limited by their respective resources in the classical density-dependent fashion.
- 2) Interspecific competition must necessarily exist among the members of each of these three trophic levels.
- 3) Herbivores are seldom food limited, appear most often to be predator-limited, and therefore are unlikely to compete for common resources."

No mention is made of the fact that "the world is green" or anything like that, but historically this paper is cited for the Green World Hypothesis [maybe stemming from Murdoch's critique?]: herbivores are predator limited, while producers are resource limited (expand to the limit of the resources) - thus plants aren't totally consumed.

**Hardin, Garrett. 1960 The Competitive Exclusion Principle *Science* 131: 1292-1297.**

**One sentence summary:** The competitive exclusion principle (two species occupying the exact same niche and geographical space, cannot exist) is an important, and widespread way of thinking.

Hardin clarifies why the exclusion principle, in abstract, *has* to be true.

The philosophy behind it:

The theory cannot be proven, or disproven,

1. Because of the 'axiom of inequality': no 2 things can be exactly identical, anyway.
2. Because you can never be absolutely sure of your niche definitions.

This limitation is acceptable, if you're aware of it. More useful to test the theory in a *broader context* of a *system of theories*.

Origins of the theory: Going back through time: Lack, Gause, Lotka, Volterra, others?  
 Keynes (economics), Bertrand (mathematics)  
 Darwin touched on it, but didn't nail it.

Applications abound:

Economics: the phenomenon of monopolies  
 Genetics: alleles competing; one would eventually exclude all others at a site  
 Ecology: marvel at the unlikelihood of diversity!

Conclusion: we will have a renaissance of thinking in all these fields when we explicitly accept the clear reality of the competitive exclusion principle.

**Hassell, May, Pacala, and Chesson.** 1991. The persistence of host-parasitoid associations in patchy environments: I. A general criterion. *Am Nat.* 138(3): 568-583

**One Line Summary:** They proposed a very general criterion for stability of host-parasitoid systems: that the  $CV^2$  (density of parasites that hosts experience) is greater than 1. They show that this criterion holds for 5 different discrete host-parasitoid models.

There are two extreme ways that hosts can experience variance in parasitoid density.

HOST DENSITY DEPENDENT: the density of parasitoids varies as a function of host density.

HOST DENSITY INDEPENDENT: density of parasitoids varies as a random variable, unrelated to host densities.

The proportion of hosts that escape parasitism is the critical quantity that leads to determining stability.

The authors derive this stability condition from 5 discrete models:

1. HDI - parasitoid density varies from patch to patch as gamma-distrib rand. var.  
 - host density is random too, and the two are unrelated.
2. HDD - host density varies from patch to patch as gamma distrib rand. variable.  
 - parasitoid density tracks that of host with perfect correlation
3. HDI and HDD combined - general model covers any degree of correlation between host and parasitoid densities.
4. No Spatial Structure - the variance in proportion of hosts escaping parasitism isn't due to spatial variation, but to variation in hosts' ability to survive infection. So the CV condition isn't just for *spatially* caused variation.
5. HDI with Dispersal - Model 1 had complete redistribution of hosts and parasitoids after each generation. Here we have hosts evenly distributed, and parasitoids randomly colonizing after emerging.

Q. What kinds of spatial heterogeneity give stability?

- A. ANY kind, from HDI to HDD, as long as the variability in parasitoids satisfies  $CV^2 > 1$ .  
 (when using discrete models, totally host-specific parasitoids, random host choice, and no interference/competition)

**Pacala and Hassell,** 1991. The persistence of host-parasitoid associations in patchy environments: II. Evaluation of field data *Am Nat* 138(3): 584-605.

**Few-Line Summary:**

- In this companion article, they provide methods of estimating the parameters of the previous models, using real data. This includes partitioning the CV of parasitoid density into HDD and HDI components. (host-dependent and host-independent variation)

- The analyzed 34 studies this way, and found that 1/3 of them had a  $CV^2 > 1$ , adequate for stability. In 90% of the cases with  $CV^2 > 1$ , HDI was more important than HDD, confirming that theoretical prediction of Chesson and Murdoch (1986).

**Holt, R.D. & Lawton, J.H.** 1994. The ecological consequences of shared natural resources. *Ann Rev Ecol Syst* 25: 495-520.

**The main point:** I'm not sure, this was a confusing article! The most I got out of it was the definition of some terms. The point I took home was that short and long term studies may reveal different consequences of shared predation, e.g. keystone species (apparent mutualism) effect vs. apparent competition

Some definitions: apparent competition = competition for enemy-free space. When more than one victim (prey, host, etc) share at least one enemy (predator, pathogen, etc). This means that an increase in prey 1 abundance, increases the predator density which thereby reduces prey 2. Thus an increase in prey 1 causes a decrease in prey 2, which is how the phenomena got the term "apparent competition", because the consequences are the same as interspecific competition, but they are really being affected by an indirect interaction via a shared predator.

The core criterion for a another victim species to invade a community with a resident enemy:

$$r > aP$$

where

r = invader growth rate

a = attack rate of predator

P = ave predator abundance

Short term studies may see an indirect positive interaction between two victim species who share a predator (keystone species idea), which if examined over longer periods, may actually be an indirect negative interaction (competition for enemy-free space).

**Hubbell** 1997. A unified theory of biogeography and relative species abundance...

Introduction: Hubbell sets up some dichotomies:

- Ecologists vs. Biogeographers
- small-scale processes vs. large-scale processes
- niche assembly vs. dispersal assembly
- the species matters vs. competitive equivalents

theory of island biogeography says nothing about relative species abundances theories of relative species abundance say nothing about number of spp. in community

Assumptions:

metacommunity provides migrants & where speciation occurs

local community: max. patch size for which dispersal limitation can be ignored

species arise as point mutations (initially rare)

homogenous environment

identical species

zero-sum community dynamics

saturation: individual must die before space is opened up for a new recruit

Basic point: assuming perfectly homogenous environment w/ identical species, can have a rich community.

Dominance arises by chance and not by competitive superiority.

Theory simplifies to 3 parameters, none of which are species-specific:  $\theta$  (Theta), J, m.

Theta: fundamental biodiversity number =  $2Jmv$  where  $Jm$  = no. individuals in metacommunity and  $v$  = speciation rate.

J = local community size (no individuals)

$m$  = migration rate

Theta is higher for tropical forests.

Unified theory can generate dominance-diversity curves that match BCI and Pasoh data, via "best-fit theta values" and an arbitrarily chosen  $m$ . Why should this impress us? I don't understand how it can be predictive because theta is essentially unmeasurable; how do you define the metacommunity so you can count  $J_m$ ? How do you measure speciation rate?

Dynamics of model:

1. If metacommunity abundance is low, high probability that local abundance is low as well
2. When migration rate is large (near 1), then the abundance of any particular species locally is likely to be near its abundance in the metacommunity (more slop for lower  $m$ )
3. As  $m$  decreases (isolation increases), rare species get rarer and common species get more common.

**Huston 1979.** A general theory of species diversity. *Am Nat* 113:81-101.

Presents Huston's "dynamic equilibrium model" which is verbal/graphical. Like Connell, he argues in favor of nonequilibrium models of species diversity and against the niche-assembly view. Connell (1978) cited this paper as in press and viewed Huston's model as an "extension" (special case) of the IDH.

Two main ideas:

- 1) diversity is highest at intermediate frequencies of disturbance (cites Connell and others)
- 2) diversity is highest at low (but nonzero) population growth rates of the community. At  $r = 0$ , no species can survive; at low  $r$ 's, many species coexist and diversity is high; at high  $r$ , competitive exclusion happens quickly and low diversity results. Graphing disturbance frequency vs. growth rates gives a graph of elliptical isoclines in which diversity is highest near (but not at) the origin, and lower as you move towards higher rates of growth and frequencies of disturbance.

This model purportedly explains the paradox of enrichment. If enrichment increases population growth rates, then competitive exclusions are hastened and diversity declines. It also purportedly explains productivity/diversity gradients; high productivity "reflects" high population growth rates and thus low diversity is predicted. Huston cites many examples which could be consistent with this (e.g. marine plankton have much higher diversity, but lower density and productivity, in tropical vs. temperate waters), but does not demonstrate any causal mechanisms.

**Huston, M., and T. Smith.** 1987. Plant succession: life history and competition. *American Naturalist* 130: 168-198.

**One-sentence summary:** Think of succession in terms of competition between individuals whose life-histories are constrained by tradeoffs. Possibly a more useful paradigm than population-level models of succession.

The authors suggest that a useful approach to modelling succession is based on *competition* between *individual* plants, within which *tradeoffs* between traits confer competitive dominance to different species under different conditions. They suggest that an individual-level model of succession, rather than the population-level models of succession such as the modified Lotka-Volterra model of interspecies competition and Tilman's (1985) "R\*" model of plant competition, may be able to account for many of the "atypical" successional patterns seen in nature (e.g., cyclic replacement) as well as classic succession.

The authors propose a set of life-history trade-offs such that a plant which is a competitive dominant under one set of conditions cannot be a competitive dominant under other sets of conditions (e.g., the classic r-K, early-succession/late-succession contrast). By creating "species" with various combinations of five traits and running simulations of light competition between the various pairs, they manage to simulate realistic patterns of "classic" as well as "atypical" succession. This model can be modified to incorporate other limiting resources and can model non-equilibrium as well as equilibrium processes. Basically, the upshot seems to be that an individual-based model

is much more flexible and realistic than population-based models and can successfully simulate a broader range of phenomena. However, the authors note that these models are much more complicated than population-level models and, for some purposes, the added resolution is unimportant.

**Hutchinson, 1961.** Paradox of the Plankton *Am. Nat* 95: 137-145.

Many many species of Phytoplankton occur together in unstructured environment  
(large or very small volumes of water have diverse assemblages)

Competitive Exclusion doesn't explain the magnitude of diversity  
Competitive Exclusion predicts different species abundance patterns than exist.

Other contributors to species richness

**Symbiosis and commensalism** - some examples do exist

**Predation** can allow 2 spp (under different predation pressure) in same niche to coexist.

**Non-Equilibrium:** due to nature of sea and lake systems, equilibration never happens  
"opportunistic community"; you'd predict chance extinction to have role.

**Inoue, K. 1993.** Evolution of mutualism in plant-pollinator interactions on islands. *J. Biosci* 18: 525-536.

Comparative & fairly anecdotal study of plants & pollinators on mainland Japan and the Honshu islands shows evidence that pollinator limitation has driven plant distribution and evolution, and vice-versa. The islands are volcanic & were never connected to the mainland. Bumblebees are the major long-tongued pollinators on the mainland, but they are absent on all but 1 of the islands. Most mainland plants dependent on bumblebees are absent from the islands, and those that are present have smaller flowers (assumed to increase pollination efficiency by the smaller, short-tongued, non-bumblebee pollinators that are present). Island plants are more self-compatible, and produce more, smaller seeds than their mainland conspecifics/congenetics. Phenologies have shifted as well.

**Janzen 1970.** Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501-527.

The classic source for the "escape hypothesis." Recognizes that Ridley (1930) suggested many of the patterns and mechanisms of the escape hypothesis. The word "escape" is used several times but not "escape hypothesis."

"For most species of lowland tropical trees, adults do not produce new adults in their immediate vicinity (where most seeds fall)... the number of seeds of a given species arriving at a given point in the forest usually declines with distance from the parent tree(s)...the negative effect of [host-specific plant parasites and predators] on population recruitment by the adult tree declines with increasing distance of the juvenile trees from their parent and other adult trees." Predators are seen as preventing competitive exclusion. Regular spacing (rather than clumped or random) should result if this mechanism works.

The classic graphical model presented: distance from parent tree (x-axis), number of seeds per unit area (called "I" for "immigration", y1 axis), probability that seed or seedling will mature (called "P", y2 axis). A "population recruitment curve" appears at an intermediate distance from the parent tree, peaking where the I and P curves have their maximum product. This model is redrawn several different times to show effects of different disperser types (change shape of I curve), different levels of predispersal seed predation, etc. 5 hypotheses are suggested for testing (seed survival should be increase with distance from the parent, etc.) but they all seem to follow directly from the basic argument.

Cool 3-d maps of seed shadows and 2-d maps of "crater rims" of recruitment surrounding adults. Suggests that proximity to male vs. female trees can generate different patterns in seed/seedling survival. Interesting contrast of "ecological distance" vs. "geometric distance" in reference to predators finding plants; 300m in a contiguous habitat is much shorter ecologically than 300m between a ridgetop and valley bottom.

**Janzen, D.H.** 1967. Why mountain passes are higher in the tropics. *Am Nat* 101: 233-246.

**One sentence summary:** there is a relationship between climate uniformity and the ability of organisms to cross adjacent areas, e.g. mountains, with different climatic regimes.

Mountain passes are figuratively higher (more effective) in the tropics because:

1. The temperature gradient, not elevation, is what determines a mountain's effectiveness as a barrier.
2. There is shorter range of temperatures in the tropics (more constant temp) than temperate regions (more variable temperature).

Key variable: the amount of overlap between the range of temperatures at the top and bottom of mountains. Overlap in temperature (between tops and bottoms of mountains) in temperate regions >> overlap in temp in tropics

organisms living in a more constant environment cannot handle change as well as organisms living in a variable environment.

Therefore, organisms in temperate regions (who experience more varied temperature regimes) can cross mountain barriers more effectively than organisms in the tropics.

**Janzen, D.H.** 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104: 501-528.

**One-sentence summary:** Janzen hypothesizes that relatively host-specific seed/seedling predators which home in on high host-plant densities or on parent trees can prevent recruitment near the parent. This would produce a widely spaced tree population and allow a high diversity of trees to live together in tropical forests.

Janzen postulates that a lot of tropical seed or seedling predators (organisms which kill seeds or seedlings) are specific to one or a few tree species and that they respond either positively to host-plant density or negatively to distance from the parent tree. The result is that, even though a lot of seeds may fall near a parent tree, maximum recruitment occurs at some *intermediate* distance from the parent. The result is a cap on the density which any one species can attain. This leaves a lot of room for other species to pack themselves in—in other words, high tree diversity is maintained by attack by consumers.

The jury is still out on the Janzen-Connell mechanism (Connell came up with the same idea independently in a 1971 paper) after nearly thirty years. The hypotheses are hard to test, and research on the subject has neither rejected nor resoundingly confirmed them. The mechanism seems to be true for some tree species in some places, but it's far from clear that it can really account for the enormously high diversity of trees in the rain forest.

**Keddy** 1991. Plant competition and resources in old fields. *TREE*

Discusses Tilman's recent tests of  $R^*$ : 5 perennial grass species grown on a soil fertility gradient.

TILMAN IN A NUTSHELL:

N is the principal limiting resource in terrestrial plant communities. Light is the principal limiting above-ground resource. These are often negatively correlated in nature. Therefore, N-light ratios are a key feature that describes the resource state of a particular community.

Predictions:

- 1) the species that can create the lowest level of the limiting resource ( $R^*$ ) will exclude other species.
- 2) species differ in the ratio of their above- to below-ground competitive abilities, and this determines which species will eliminate others in a particular habitat.

RESULTS

- 1)  $R^*$  determined by measuring soil N under grasses grown in monoculture.

R\* differed significantly betw. spp. at low N, but not at high N => plants might compete by lowering soil N, at least at low N.

- 2) Root biomass explains 73% of the variance in R\* (more roots let you more efficiently extract N)
- 3) Low R\* species "strongly suppressed" high R\* species (sample size of only 4 species though) => evidence that competition works in a Tilmanian way
  - a) the closer the R\* values of the competing spp., the longer it took to see suppression
  - b) same results irrespective of soil nutrient status, suggesting invariant competitive hierarchies
- 4) Early successional species had higher R\* for N than later spp. This falsifies the resource ratio hypothesis, which proposes that early spp. are better N competitors while later spp. are better light competitors. Supports the alternate hypothesis that there is a tradeoff between competitive ability and colonizing ability.

**Louda, S. M.** 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs* 52:25-41.

**One sentence summary:** Insect predators can strongly influence the distribution and abundance of plants. The shrub *Haplopappus* (Asteraceae) exists in a gradient of increasing abundance from the coast to the mountains near San Diego. The reverse trend is expected from flower abundance (assuming that recruits are proportional to flowers, each of which produces a single seed). Seed predation is carried out by a diverse guild incl. lepidopterans, dipterans, and thrips. Insect predation is greatest in the coastal zone.

Experimental insecticide treatments (and monitoring of seedling establishment, survival, and recruitment) were carried out to see if the gradient could be caused by seed predation. The greatest increase in seed survival was on the coast. Seedling recruitment was directly related to post-predation seed number, not to juvenile or adult numbers. Abundance of each age class was related directly to the abundance of the previous age class. Thus, predation explained the gradient (competition and abiotic conditions were ruled out as per-capita survival in the coastal zone was equal to that in the interior).

[I say: Related to Janzen/Connell mechanisms but with some twists: 1) diverse guild of predators, not a single specialist; 2) distance from parent not measured; 3) predators not acting solely in response to plant density (anecdotally, moth densities appeared to be higher on the coast, where plant density was lowest); but, since no. of flowers per plant is greater at coast, are they responding directly to seed density?]

**Lubchenco** 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am Nat* 112:23-39.

Applies to both FOOD WEB and HERBIVORY topics. Inspired by Paine's keystone predator hypothesis, but with an herbivore (a snail, *Littorina*) instead of a carnivore. Massachusetts coast.

1. In tide pools, humped relationship between snail density and diversity.
  - a) low densities of the snail result in competitive displacement and low diversity
  - b) intermediate densities promote high diversity via preferential grazing on the algal competitive dominant
  - c) high densities result in the removal of most algal individuals and spp. and low diversity.
2. On emergent substrata (exposed at low tides), linear relationship. increasing densities result in decreasing diversity.

Why? the competitive dominant in tide pools is an undefended algae, yummy to snail. On emergent rocks it is a hardy perennial, yucky to snail. There, it eats the competitively inferior species and indirectly increases the dominance of the perennial algae.

**Lubchenco, J.** 1978. Plant species diversity in a marine intertidal community: importance of herbivore

food preference and algal competitive abilities. *American Naturalist* 112: 23-39.

**One-sentence summary:** Herbivore food preferences interacted with competitive abilities of the food plants to determine how herbivory affected species diversity. Where the herbivore's favorite food was competitively inferior, an intermediate level of herbivory allowed maximum diversity; where it was competitively superior, herbivory always caused a decline in community diversity.

Lubchenco studied the alga-eating periwinkle snail *Littorina littorea* along the New England coast. In tide pools, where the competitively dominant alga was a fast-growing, highly palatable species (*Enteromorpha* spp.), the relationship between herbivory and species diversity was much like that described by Bowers (1993): at low levels of herbivory, the competitive dominant excluded everything else; at very high levels it ate everything except a few unpalatable species; at intermediate levels, herbivory and competitive exclusion balance one another to produce a maximally diverse community. (Imagine a curve shaped like a haystack.) However, on emergent substrate the competitive rankings are reversed; the competitively dominant alga is now a species (*Chondrus crispus*) which the snail can't stand. In this situation, herbivory only reinforces the dominance of *Chondrus*, and community diversity decreases monotonically with increasing herbivory. (Imagine a line heading downhill from left to right.) Potentially, herbivory can increase *or* decrease community diversity, depending on 1) how herbivore preferences and competitive dominance interact, and on 2) how intense the herbivory is.

A bonus: Lubchenco notes that, if *Enteromorpha* gets really well established in the tide pools (i.e. snails are absent for a long time, for whatever reason), green crabs can establish themselves in the dense cover where gulls can't get at them. The crabs eat immature snails. The upshot is that an *Enteromorpha*-dominated community, if it gets established, is stable because snails can't invade and eat the dominant alga. If snails *are* present, *Chondrus* dominates because of its unpalatability. So there is the possibility of multiple "stable states" in the tide-pool community, depending on whether or not snails get in before a thick *Enteromorpha* cover develops. Note that Lubchenco is suggesting that the algal community may be heavily influenced by the *fourth* trophic level, the gulls.

**MacArthur, R.** 1960. On the relative abundance of species. *Am Nat* 94: 25-36.

**Strong's summary:** formalization of niche theory (dead end). hypervolume, broken stick model.

MacArthur compares opportunistic versus equilibrium species, is interested in equilibrium species. Tests predictions of species abundance from overlapping versus non overlapping niche theories. Concludes that the total number of individuals of all species is constant and that niches are non overlapping.

**Opportunistic species** (r-selected): relative abundance controlled by "vagaries of climate". Not interested in these kinds of species for relative abundance theory.

**Equilibrium species** (K-selected): two alternatives:

1. total number of individuals of all species essentially constant. Suppose there are 10 individuals and 4 species, can draw vertical bars to delineate species. *Non overlapping niches*.

|iii|ii|iiii

An increase in abundance of one species (change in position of one of the vertical bars) automatically involves a corresponding decrease in the abundances of other species.

2. Abundances of different species are independent. An increase in abundance of one species doesn't affect other species' abundance. *Overlapping niches*.

Compared bird species abundances with predictions of (1) and (2). Found more agreement with (1).

Though MacArthur didn't use the term, a **broken stick** describes the way in which niches are distributed among species (non-overlapping), the length of the broken segments set by the number of individuals of each species. is this right?

**Mazumder, A.**, 1994. Patterns of algal biomass in dominant odd-vs. even-link lake ecosystems. *Ecology* 75:1141-9.

**Two-sentence summary:** Top-down or bottom-up regulation of phytomass? The answer suggested by this article is yes and yes: according to data from north temperate lakes, algal biomass increases with potential productivity faster when planktivorous fish are plentiful to consume herbivorous zooplankton (top-down), but it does increase even if carnivores are rare (bottom-up); in neither case does algal biomass increase linearly with potential productivity, contrary to current models.

This article presents a test of trophic-level regulation models using data from north temperate lakes. The focus is on how plant (algae) biomass, measured as chlorophyll concentration, varies with potential productivity, measured as phosphorus concentration, in lakes with or without a significant carnivore (planktivorous fish) trophic level. According to top-down models, such as that of Oksanen et al., 1981, in carnivore-poor lakes, phytomass should plateau as productivity increases, the increased productivity being absorbed by a growing population of herbivores (algae-eating zooplankton), while in carnivore-rich lakes, phytomass should increase steadily as productivity increases, the increased productivity being absorbed by a growing population of carnivores that regulate the herbivores---the HSS hypothesis, by any other name. In contrast, according to bottom-up models such as that of Ginzburg and Akcakaya, 1992, phytomass should increase steadily as productivity increases, regardless of whether carnivores are abundant or scarce, the impact of one trophic level on the next one down being negligible by comparison with the impact of primary resource limitations. Fig. 4b and c on p. 1 of the notes on lecture 7 by Strong indicate the contrast.

Mazumder surveyed the limnology literature, classifying lakes as carnivore-poor or carnivore-rich (my terms---I find his “dominant even-link” and “dominant odd-link” less satisfactory) primarily according to presence or absence of large *Daphnia* spp., which planktivorous fish tend to snap up. In each of these classes, he regressed chlorophyll concentration on phosphorus concentration; the data points, one per lake per year, and the regression lines are plotted on p. 3 of Strong’s notes. He further subdivided each class into low-, medium-, and high-phosphorus concentration subclasses and did the regression in each of these subclasses, seeking the ‘stair-step’ pattern predicted by top-down models.

He forms three main conclusions:

- (1) As predicted by top-down models, phytomass increases (significantly) more with productivity in carnivore-rich lakes. Thus “plants attain greater densities when grazers are controlled by the primary carnivores such as planktivorous fish in lakes.” (p. 1145)
- (2) As predicted by bottom-up models, phytomass increases (significantly) with productivity even in carnivore-poor lakes. Thus “increased resource availability produces higher algal biomass even when grazers are released from their predators.” (p. 1146)
- (3) As predicted by no current model, the increase of phytomass with productivity is generally nonlinear. Whereas the first two main conclusions are evident from the figure in Strong’s notes, this one is more evident in the subclass analyses.

A problem with the study is the use of phosphorus concentration as a measure of potential productivity. It leads to the conclusion, evident from the figure in Strong’s notes, that “[o]verall, the [carnivore-rich] ecosystems yields significantly greater algal biomass than the [carnivore-poor] ecosystems regardless of the potential productivity.” (p. 1146) I suspect carnivore density is correlated with some other variable, which maybe should be aggregated with phosphorus concentration as a measure of potential productivity, or more likely the situation is too complex to be understood in such a simplistic way.

**Menge, B.** 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65: 21-74.

**One sentence summary:** indirect effects (defined as effects of species A on C via direct effects of A on B and B on C) in 23 intertidal habitats were important, accounting for 24-61% (average 40%) of the change in abundances (summed across all species) following experimental manipulations. The 40% appears to be independent of the species richness of the web. These indirect effects fell into 9 general categories (7 of which are summarized in the

arrow diagrams reproduced in Don's handout, Lecture 8, p. 1); keystone predation (KP) and apparent competition were the most common while exploitation competition was least common.

Interestingly, trophic cascades (TC's) were uncommon. Menge suggests that KP and TC are qualitatively different versions of the same interaction; TC's occur in pelagic communities, while KP occurs in benthic [mechanisms are different; the middle species in TC consumes the basal species, while the middle species in KP competes for space with basal species].

Some impt. definitions:

- 1) "interaction web" includes only species that have been identified experimentally as interacting strongly. Includes both trophic and non-trophic interactions. Contrast with "food webs" (include all species, depict consumer-prey links only) and "energy-flow webs" which trace energy, biomass or nutrients.
- 2) "basal species" are those sessile primary space holders (both animals & plants).

This is a truly massive monograph; here's the abstract:

**ABSTRACT.** To determine the patterns of occurrence and importance of indirect effects relative to direct effects in natural communities, I analyzed experimentally based studies from 23 rocky intertidal habitats. The vehicle of analysis was the construction of interaction webs, or the subset of species in food webs involved in strong interactions. The analysis focused on indirect effects involving changes in abundance, or interaction chains. Since little information was available on other types of indirect effects (behavioral, chemical response, environmental). As expected, number of direct (= strong) interactions, indirect effects, interaction sequences producing indirect effects, and types of indirect effects (e.g., keystone predation, apparent competition, etc.) all increased with web species richness. Less expected, when these measures were adjusted to a per species basis, positive relationships with species richness were still observed for all measures but the number of types. In other words, with increasing web diversity, each species interacted strongly with more species, was involved in more indirect effects, and was part of more interaction pathways. The analysis identified 83 subtypes of indirect effect, including the seven previously identified types. Many of the 76 additional types could be reclassified into the seven types if the original definitions of these "classic" types were expanded to include interactions having similar effects but differing in the specific mechanism (e.g., both interference competition and inhibition of recruitment (preemption) have negative effects involving a spatial resource). Two new types of indirect effect, termed "apparent predation" and "indirect defense" were also identified, producing a total of 9 general types of indirect effect divided among 565 specific indirect effects. Of these, keystone predation (35%) and apparent competition (25%) were most common and exploitation competition (2.8%) was least common in these webs. Two methods of analysis suggested that indirect effects accounted for approximately 40% of the change in community structure resulting from manipulations, with a range of 24-61%. The proportion of change due to indirect effects was constant with web species richness, indicating that strong direct interactions and indirect effects produce roughly the same level of alteration of community structure regardless of the level of web complexity.

Several potential artifacts and biases were evaluated. Most importantly, neither variation in level of taxonomic resolution nor intensity of experimentation varied significantly with web size (species richness). Despite a bias toward manipulation of consumers over manipulation of basal species, some predator-initiated indirect effect types were scarce while some basal species-initiated types were common. While the frequency of exploitation competition may have been underestimated, it is unlikely that the frequency of this indirect effect would change dramatically: changes due to this effect should have been detected in many of the studies and reported; and the most intensively studied individual webs did not report frequencies differing much from the average. This analysis suggests investigators effectively identified and first manipulated those species responsible for most indirect effects and that more experiments added decreasing numbers of indirect effects. Moreover, the frequencies and importance of indirect effects may be more predictable than expected on the basis of theory.

**Murdoch 1966.** "Community structure, population control, and competition" -- a critique.

Finds fault with assumptions and logical structure of HSS.

#### HSS Assumptions

Murdoch says herbivores are not food-limited because plants are not "eaten out" {Murdoch's words} not all green plant material may be edible (implies plant defenses) and/or organisms may be food-limited without depleting their food supply implies that there are only three ways in which herbivores can be limited:

food, weather, predation there are other possibilities for limitation:

- resources other than food (eg nesting or oviposition sites)
- "self-regulatory systems" [not explained; DRS says cannibalism, territoriality]
- relative shortage of food (cites Andrewartha and Birch 1954; this is probably the precursor to Erlich & Birch 1967).

implies that all species of herbivores can reduce green matter Points out that many species of herbivores cannot deplete green matter in general (eg pollen and fruit-feeders); thus HSS arguments do not apply to them (may be limited by something other than food).

#### Logical Structure:

Points out that the same type of evidence was used to reach opposite conclusions: plants are not "eaten out" so herbivores are not food-limited; yet even though herbivores are not eaten-out either, carnivores are food limited. [I can't see how HSS would get out of this].

Applies Popper's criterion of falsifiability; since the HSS hypothesis cannot be disproved, it must be restated. DRS says Murdoch is the first to use Popperian arguments in ecology. How would HSS hypotheses be tested? It is clear that showing a single herbivore population, or group of herbivore populations, to be food-limited would still not disprove HSS; showing that the entire herbivore trophic level is food-limited is necessary. However, because "trophic levels exist only as abstractions, and unlike populations they have no empirically measurable properties or parameters", HSS is not falsifiable.

HSS uses weak definitions and needs to be operationalized; only experimental tests of rigorously stated hypotheses will advance ecology out of its "present non-rigorous state."

**Murdoch, W.W. and J. Bence.** 1987. General Predators and Unstable Prey Populations In a book, *Direct and Indirect Effects on Aquatic Communities*.

#### One Line Summary:

In predator-prey systems in which the predator is a generalist, many of the normal forces that stabilize predator-prey systems do not work. This is commonly seen in aquatic systems, where generalists drive prey extinct.

In these situations, predators often drive prey extinct.

Prey cannot effectively regulate predator increase.

Both short-term and long-term modes density-dependent regulation don't work.

Numerical response: cross-generational conversion of prey into new little predators. LONG TERM

Any one prey species cannot regulate this because in general:

- there are other prey that the predator is utilizing
- in these aquatic systems, the predator is usually longer-lived than the prey

Ruled out as source of possible stabilization.

Functional response: the actual within-generation pattern of consumption. SHORT TERM

This is the other possible source of stabilization.

Most aquatic generalist predators are 'dumb': they don't ignore prey even when it becomes very rare. That gives Type II → destabilizing.

If fish learn, and quickly switch prey when the focal species becomes rare:

Type III → conditional stability, depending on how fast they learn.

BUT: If there's a time lag in learning, it's still destabilizing

Other prey stabilizing possibilities OTHER than predator: REFUGES!

Gives what appears to be a Type III functional response, and can give stability.

Perhaps because of the simplicity of the aquatic env., you see less stabilization than in terrestrial systems

**Nunney, L.** 1980. The influence of the Type 3 (sigmoid) functional response upon the stability of predator-prey difference models. *Theor Pop Biol* 18: 257-278.

**The main point:** the stabilizing effects of a Type III functional response has already been demonstrated for continuous time models. Nunney extends this generalization to discrete time models.

**Remember:** *Discrete time* models use *difference* equations. Without Type III response, these models are unstable and result in oscillatory behavior. *Continuous time* models use *differential* equations. The *functional response* of a predator to its prey defines the way in which the capture rate of a predator changes with the level of the prey. *Type III* is a sigmoid-shaped curve, and could result from something like a search image (predator efficiency poor initially, improves with experience and then levels off, or becomes limited by handling time).

The main models he's concerned with look like:

$$P_{t+1} = P_t F(x_t)$$

$$R_{t+1} = r S_t$$

Where P = predator, R = resource, F(x) is the predator's conversion efficiency to convert prey into predators, r is the resource growth rate. This model is different from the discrete time Nicholson Bailey Host Parasitoid (N-B) equations because N-B assumes that the parasitoids can't detect the changing abundance of hosts, whereas predators in this model "experiences the absolute decline in prey population between generations." A type III response cannot stabilize the N-B model.

**The stability conditions are:**

$$\frac{dG}{dR} > \frac{G(R)}{R}$$

Where dG/dR = change in functional response with resource density, G(R) = functional response, R = prey density. This condition is not satisfied for Type I or Type II functional responses with this model.

Nunney adds the following modifications to the model, with only minor changes to the stability conditions:

- prey self-limitations
- how important is food consumed outside the breeding system on predator efficiency (has no or little effect)

Nunney's **summary**: "including a type III functional response in a difference model of predator-prey interactions, either with or without prey self-regulation, exhibits the characteristics stabilizing influence of such a response found in continuous models. This result strongly supports the view that type III functional responses can act in natural systems to promote local stability. Furthermore, it has been shown that systems can be locally stable even when the prey species has a very high reproductive rate and prey self-regulation is absent."

**Oksanen, L., Fretwell, S. D., Arruda, J., and Niemela, P.**, 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240-61.

**Two-sentence summary:** See Fig. 4b on p. 1 of the notes on lecture 7 by Strong---this picture is worth the thousands of words in this article. The authors claim their picture is more consistent with data than the picture of Fretwell, 1977, which is Fig. 4a in Strong's notes, in that phytomass seldom decreases but often plateaus as potential productivity increases.

This article has two main parts, the first presenting theory and the second comparing theory with data. The theory is an analysis of the equilibrium point of a dynamical system with three dependent variables representing plants (P), herbivores (H), and carnivores (C). The P-equation contains a logistic term and a Holling type-two functional

response term representing herbivory; the H-equation contains a corresponding numerical response term, a constant death-rate term, and a Holling type-two functional response term representing carnivory; the C-equation contains a corresponding numerical response term and a constant death-rate term. The authors not only present little motivation for these choices, but they also do not even write out the H- and C-equations---one surmises what they must be. Setting to zero  $dP/dt$ ,  $dH/dt$ , and  $dC/dt$  yields P-, H-, and C-isoclines, surfaces in (P,H,C)-space whose intersection is usually the unique equilibrium point of the dynamical system. Finally, it is assumed that plant intrinsic growth rate and carrying capacity (recall there is a logistic term in the P-equation) are directly proportional to a variable G termed “potential productivity.” The authors then analyze how the equilibrium point moves around in (P,H,C)-space and how its stability changes as G varies. The results are represented in Fig. 4b on p. 1 of the notes on lecture 7 (Food Webs II) by Strong, more concisely than in the article itself. One wrinkle omitted from the figure is that in some intervals of G, the equilibrium point may be unstable. The main point of interest to the authors is that in their model, equilibrium P plateaus in some intervals of G, but it never decreases as G increases, in contrast to the model of Fretwell, 1977, which is Fig. 4a in Strong’s notes.

The second part quotes lots of data, none in more than very rough agreement with the theory. Probably the main point is that the data do not seem to support the prediction of Fretwell, 1977 that in some intervals of G, equilibrium P decreases; at worst, it plateaus, as predicted by the theory above.

**Paige, K. 1992.** Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. *Ecology* 73:2076-2085.

Monocarpic scarlet gilia (*Ipomopsis*) in Arizona and destruction of apical dominance. Grazer (deer, elk) removal of the single inflorescence releases lateral buds which form an average of 5 new stalks, increasing fruit & seed production and overall fitness. For the first herbivore attack only, early herbivory results in overcompensation; late herbivory (after flowering) results in equal compensation.

The early, single stalks are high quality, while secondary stalks are low quality to deter herbivory [tested by experimentally creating single-stemmed plants from multiple-stemmed ones & recording rates of herbivory; actual chemistry- whether it’s a decline in nutrients, or an increase in secondary compounds - not investigated]. This explains why secondary grazing is limited to tips of the plant. Experimental clipping of secondary stalks reduced fitness by 70%. Thus the plants switch from a mutualistic relationship with the grazers to an antagonistic one.

Evolutionarily, it is suggested that grazing is predictable; 77% of the study plants in 5 yrs were grazed. My question: is the key to high fitness lateral dominance or timing? If it’s lateral dominance, the current situation suggests that gilia’s inability to induce lateral dominance by itself is an evolutionary quirk. Alternately, the movements of grazers might have been so predictable that the timing is the crucial thing (put all your biomass aboveground right after the grazers move through), and the current situation makes sense.

**Paine and Levin 1981.** Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* 51: 145-178.

Tatoosh Is., Washington. *Mytilus californianus* is the dominant competitor. Study focuses on the mussel beds which exist above the *Pisaster* predation line.

A model of patch dynamics is developed & tested against field data; it can correctly predict the age-size class distribution of patches. Patches are “born” with disturbance, and “die” when closed over by sessile organisms. Smaller patches are closed over by “leaning” responses of the mussels, larger patches by migration of established mussels (!?), and still larger patches by recruitment of larval mussels from the plankton. Mean turnover time was 8-35 years, depending on location.

Empirical and theoretical support for the IDH: high-disturbance sites never get high-diversity (which requires many patches of differing ages), low-disturbance sites are a monoculture of *Mytilus californianus*.

**Paine, R.T. 1966.** Food web complexity and species diversity. *Am Nat* 100: 65-75.

**Strong's summary:** "keystone predator increases local diversity by suppressing competitive dominants." Predation may prevent resource monopolies, thereby increasing diversity.

**The system:** rocky intertidal marine organisms competing for space (also see Connell 1961, Dayton 1972) north temperate (Pacific coast)

starfish ← gaspode ← barnacles  
 ←—————┘

**Methods and Results:** remove top carnivore (starfish) from one study plot and keep another as control. Saw succession by bivalves and chitons, algae all consumed. The removal of starfish resulted in a pronounced decrease in species diversity, compared to control. Area became trophically similar.

**Interpretation:** starfish eat barnacles and in so doing enhance the ability of other species to inhabit the area by keeping space open. In general, barnacles will take over the space unless predators can prevent the space monopoly.

Paine compared this site with other rocky intertidal communities at different latitudes. Tries to say something about latitudinal gradients: more predators in the tropics?

Since Paine 1966, these top predators (starfish) have been termed "**keystone species.**"

**Pastor, J. & Naiman, R.J.** 1992. Selective foraging and ecosystem processes in Boreal forests. *Am Nat* 690-705.

**The main point:** trophic cascades on land? Plants that produce easily decomposable litter are also heavily browsed (the same traits that determine litter decay also determine digestibility). Herbivores may act as "switches" determining both plant community composition and the array of litters returned to the soil. Herbivory determines plant composition, changes quantity and quality of litter, soil nutrient availability and nutrient cycles.

**The system:** boreal forests (nutrient-limited, strong herbivore effects and changes in nutrients are major factors driving succession). Early successional species (aspen) have easily decomposable litter (return N to soil) but also require lots of N, fast growing, chemically defended against herbivory only as juveniles. Aspen succeeded by spruce, which has slowly decomposing litter, does not return much N to soil, slow growing and maintain constant defense against herbivory.

Moose & Beaver: eat same things but differ in foraging strategies and have opposite effects on succession. Beaver cut down (kill) early successional species and move plant composition toward early successional stages. Moose browse early successional species (don't kill), thus hasten succession to the next stage.

**Methods and Results:** used a gap model to model these effects. Varied the strength of herbivory. Found that intermediate levels of moose browsing increased primary productivity and N availability, stimulating the growth of small aspen, while too much browsing had the opposite effect. The intensity of beaver herbivory did not affect forest response because beyond a certain threshold, an intermediate intensity of herbivory was enough to kill most aspen trees.

**Interesting things:** the effects of herbivory in these boreal forests have more long term consequences than in aquatic ecosystems because changes in plant community structure may persist for many decades (long lived trees versus short lived, fast reproducing algae in lakes!). Unlike HSS, who assumed only water and light limit plant growth, this article incorporates nutrients as placing another limit on plant growth and investigates the feedback between herbivory and nutrient cycling.

Note: this paper is less about why the world is green in the traditional HSS sense, and more about the differences between herbivores in determining that green.

**Pellmyr et al.** 1996. Evolution of pollination and mutualism in the Yucca moth lineage. *Am Nat* 148:827-847.

**One sentence summary:** In the Yucca/Yucca Moth mutualism and other obligate mutualisms (eg ant/plant), the existence of the interaction is mostly a function of preadaptations, and less so of novel, coevolved traits. "The necessity of such suites of preconditions, rather than extensive coevolution after the origin of an interaction, is a

constraint that may in part account for the rarity of active pollination systems.” The fig/fig wasp mutualism is the only other active pollination system known.

The scheme: Prodoxidae is the “Yucca Moth family”, but includes mostly taxa that do not feed on Yuccas - rather on roses, saxifrages, umbels, & other agavaceaes.

*Tegeticula* and *Parategeticula* are the actively-pollinating genera on Yuccas. Three species in the genus *Greya* are the only other pollinators in the family: *politella* and *enchrysa* passively pollinate during oviposition, and *mitellae* passively pollinates during nectar-feeding. *G. enchrysa* /*Heuchera cylindrica* provides a model for what the early yucca situation may have been like: the plant is pollinated by a wide variety of insects, still gives nectar, and seed set increases linearly with number of *enchrysa* eggs (caused by the moth moving abdomen around more, spreading pollen around more, as more eggs are laid; but this is still passive).

Four traits are posited as necessary for the Yucca/Yucca Moth mutualism:

- 1) local host specificity on the moths
- 2) oviposition into the flower
- 3) limited seed destruction
- 4) pollination-causing behavior

Phylogenetic analysis and character mapping show that 1 and 3 are basal in the Prodoxidae, 2 is independently derived twice (but more basally than the common ancestor of the two Yucca Moth genera), and 4 is novel. Thus, only pollination-causing behavior was not already present prior to the colonization of yuccas. As yucca fruit set is resource (probably water) limited, mutualism with ovipositing, non-nectar feeding moths allowed nectar production to be cut out, allowing reallocation to fruit.

**Pellmyr, O. & Huth, C.J.** 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* 372: 257-260.

**One sentence summary:** first empirical evidence for selective abortion, which is a means of stabilizing the mutualism between yucca plants and moths.

The yucca plant-moth association has been heralded as one of the best examples of interspecific obligate mutualisms but until this paper, there was no known mechanism regulating the mutualism, specifically, to protect against cheating by the moths. Yucca moths lay eggs in the plants and pollinate them. Flowers with many eggs were aborted more often than flowers with fewer eggs. However, flowers with too few eggs were not the most successful because those plants were not pollinated. This is evidence that plants select against moths that lay too many eggs or which provide low-quality pollination. This suggests a trade-off between high pollen load and low egg number.

**Peres, A. & van Roosmalen, M.G.M.** 1996. Avian dispersal of "mimetic seeds" of *Ormosia lignivalvis* by terrestrial granivores: deception or mutualism?

**The main point:** There are non competitive, mutualistic interactions in the tropics! This paper is a particularly charismatic example of one: the prevailing view was that there was a nonmutualistic (sensory deception) interaction between certain "mimetic" plants which produce very hard seeds and herbivores (herbivores got no nutritional benefit from the seeds, seeds get dispersed). Instead, granivores eat these hard seeds and use them to help digest other seeds, suggesting that the plant may not be a fruit mimic at all.

**The system:** plants in neotropics which produce very very hard, brightly colored seeds, and granivorous birds.

**Methods and Results:** behavioral observations to see who ate the hard seeds. Used equipment to determine the actual hardness of the seeds (found that the seeds could take 1 ton of pressure!!). They found that granivores, tinamous and other large birds, ate the seeds. Because there are few stones available in the tropics, they inferred that the birds used the hard seeds to help digestion.

**Problems:** Although they did find that seeds which had been soaked and filed had much higher germination success than untreated seeds, they did not actually observe what the seeds look like after passing through the gut of these birds (if they are softened and more likely to germinate), nor do they know how long they are typically kept in the

gizzard.

**Polis 1991.** Complex trophic interactions in deserts: an empirical critique of food-web theory.

**One sentence summary:** actual food webs are much more complex than the ones described by previous workers; these previous "oversimplified caricatures of actual communities" thus give us wrong ideas about how trophic interactions work.

4 major problems with webs that make them inadequate for "abstracting empirical regularities":

1. Inadequate representation of species diversity. Lumping biological species into trophic species results in depauperate webs.
2. Inadequate dietary information. Most of the chains of length one in web catalogs (herbivores w/ no predators) are simply an artifact of inadequate sampling. As an example, a scorpion's diet list showed no asymptote after 200 nights of sampling and 2000 person-hours; the 100th prey item was recorded on the 181st night.
3. Age structure. Differences in body size and resource use among age classes are often equivalent to or greater than differences among most biological species (Polis 1984). The richness that age structure contributes has been largely ignored; yet it is "paramount to community dynamics."
4. Looping. "Food web theorists dismiss loops as 'unreasonable structures' ", yet they are common in the Coachella web. Esp. cannibalism, also ontogenetic reversal of predation (eg gopher snakes eat eggs and young of burrowing owls, while adult owls eat young gopher snakes), and normal ol' mutual predation (ants in territorial battles).

The Coachella Valley (Riverside Co, Mojave desert) web

- predators eat from all trophic levels (Table 1)
- utility of "trophic level" concept (trophic level = set of organisms with common number of chain links between them and primary producers) is called into question. What trophic level are consumers that ontogenetically, seasonally, or opportunistically eat all trophic levels of arthropods in addition to plant material and vertebrates?
- longer chain lengths (6 to 11 links are common, in comparison with average lengths of 2.7-2.9 published elsewhere)
- omnivory and looping are not rare
- absence of compartmentalization
- connectivity is greater (number of interactors per sp. is 1-2 orders of magnitude higher than average from published catalogs of webs)
- fewer top predators
- prey:predator ratio is  $> 1$

Many of these characteristics are hypothesized by food web theorists to cause complete instability.

**Polis and Strong 1996.** Food web complexity and community dynamics. *Am Nat* 147:813-846.

**One sentence summary:** an empirically-based critique of HSS/EEH (empirically-based in the age old tradition of amassing examples, rather than theoretically-based via models). Consumer densities are often donor controlled; trophic cascades and top-down community regulation are relatively uncommon in nature. Trophic levels do not exist. In contrast, "Trophodynamics and the EEH each rely on the integrity of trophic levels and the existence of a single, albeit different [bottom-up vs. top-down] overwhelming mechanism that imposes structure on ecosystems."

Review of earlier ideas: the exploitation ecosystem hypothesis (EEH; Oksanen, Fretwell, Hairston & Hairston 1993) generalizes HSS to  $< 3$  trophic levels. Strong consumption leads to alternation of high and low biomass at successive levels; ATC's are the clearest examples. Even - brown; odd- green. Oksanen believes that ecosystem productivity sets the number of levels (more productive  $\rightarrow$  more levels), while H&H believe that habitat differences affecting plant competition and consumer foraging set the number of levels. Both agree that 3 on land and 4 in water are the maxima.

Polis and Strong's main points:

1) Trophic levels do not exist. Food webs are reticulate: high connectance and "multichannel" omnivory. Omnivory has two major effects:

- it diffuses the effects of consumption and productivity across the trophic spectrum, rather than focusing them at particular "trophic levels."
- acts analogously to apparent competition. Predators feeding from "non-normal" sources (e.g. fruits, grains, detritus) can increase their pops, promote top-down control and suppress "normal" prey. Herbivores can do the same (e.g. granivorous birds feeding on insects can suppress plant pops).

2) Energetics is not necessarily the most appropriate way to view food webs (contra H&H 1993). Interaction webs (desc. pop. effects) and descriptive webs (quantifying energy and matter flow) are often not congruent. Another way of saying this is that an apparently weak link (in terms of diet or energy transfer) can be a key link dynamically (e.g., parasites that regulate predator pops. but accumulate little energy). Consumer regulation of populations need involve little energy transfer and few feeding interactions.

3) Parallel webs ("shunts") have big effects on the web of interest:

a) Spatial subsidies: often, consumers in one system are subsidized via consumption from another web in a different habitat. This is a donor-controlled interaction because the consumers have no effect on the other web. Their pops are maintained at high levels, which may allow top-down effects in their "home" web not possible solely with in situ productivity.

e.g.: Polis lecture on Namibian coastal system; black widow spiders suppress herbivores on dune plants, but high spider pops are really maintained by feeding on detrital-algae-feeding flies from the marine system next door.

e.g. stream systems in which leaf-fall subsidizes herbivores, which in turn depress algae.

b) Detrital shunts. Lignocellulose is the largest product of terrestrial NPP, but only bacteria and fungi can digest it. Since only about 10% of plants is eaten by herbivores, the remaining 90% must pass through the detrital chain. This makes the HSS assumption that grazer chains are not linked with detrital chains very dangerous. In fact they are; e.g. scorpions derive 39-57% of their prey from detritivores and suppress other predators.

4) EEH cannot deal with parasites and diseases, who have a very small biomass component and are not controlled by a higher trophic level.

5) EEH ignores nutrients & their effect on food web structure (it focuses too much on energy). Nutrients cannot be "grafted" onto the bottom as another trophic level below plants.

6) EEH ignores non-trophic processes which move energy and nutrients between organisms. "We question the assumption that feeding links are the major factor structuring ecosystems."

- mutualism (mycorrhizae, other symbionts), interference, habitat modification. "Plants are embedded in trophic spectra as continuous as those of any organism; the notion that herbivores are the only heterotrophs that signif. infl. plants is false."

- non-trophic uptake of dissolved organic matter (DOM)

- herbivores fertilizing plants via defecation.

7) ATC's are the "exception that proves the rule." These only occur under a restrictive set of conditions, the most imp't of which is that (compared w/ land plants) most algae are not well-defended (low noxious cmpds, no lignin). Thus herbivores can consume most of the biomass & the detrital shunt is unimportant. This sets up strong interactions & the potential for top-down control. Also implicated is the fact that aquatic media are "homogeneous" and therefore even the herbivores (eg Daphnia) are all accesible to predation, increasing the strong interactions. Systems where algae are well-defended (eg noxious cyanobacteria) do not show ATC's.

**Trophodynamics:**

1. No consumer control
2. Lowest trophic level has highest biomass generally
3. "Bottom up control"

**EEH**

- Even trophic levels = brown world
- Odd trophic levels = green world
- 1 to 4 levels with a maximum of 3 on land and 4 in water.
- Energy flow defines trophic levels
- Ignores detritious
- Consumer control
  - Works on with specific criteria
    - increasing resources  $\Rightarrow$  increasing consumption
    - Limited extrinsic factors on consumers
    - Density dependence does not affect control
    - No subsidies to consumer energy

**Complex Webs**

- Highly connected
- Omnivory
  - Even in plants
  - e.g. mixotrophic phytoplankton, symbiotic heterotrophs
  - most consume 5-100 spp.
  - cannibalism
  - Detrivore feed off all levels
  - diffuses consumption/production
  - Acts like apparent competition
- Energy flow is not informative
  - e.g. Parasites and pathogens
  - Trivial consumption can radically alter population of prey
- Subsidized Donor control
  - Spatially subsidized dynamics
- Detritus is funneled into web by predators consume detrivores
- Life history can have -/+ effects on top down control
- Most links are donor controlled
- Disease does not have a trophic level
- Nutrients affect food web variation
- Ecosystems have structure from mutualism / habitat mod /symbiosis
- Nontrophic nutrient uptake
- Nutrient rich water
- Defenses against consumption
- Mix of Donor/Recipient control

**ATCs**

- Uncommon, but support EEH
  - Algae differ from most plants
  - Completely vulnerable to predators
  - Limited detrivory

**Polis, Gary 1991.** Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am*

Nat 138(1): 123-155.

**One sentence summary:** Polis described a very complex desert food web. His aim was to show that most published food webs are grossly oversimplified, and the theoretical generalizations drawn from them are inaccurate.

Stability analysis has generated “assembly rules” for communities based on inadequate descriptions of trophic interactions.

- Pimm, Cohen are the chief perpetrators. Briand, Schoenly also.

**First, how are the published food webs inadequate?**

**1) Inadequate representation of species diversity: lumping**

- Lumping of species assumed to be on same trophic level
- Plants, microbes and invertebrates most often lumped

**2) Inadequate dietary information**

- other webs have
- other webs claim 29-47% of animals are top predators
  - \*Polis doesn't find *any* that aren't eaten at *some* life stage!
- published foodwebs don't recognize that omnivory is very common
  - \* most species eat, and are eaten by, 10-1000 other species!

**3) Age structure**

- \* Diff. ages act on different trophic levels! This has huge effect!

**4) Looping:**

- others claim loops don't exist, or just don't include them
  - \* Loops are common! For example
    - \* ontogenetic reversal: adult A eats baby B; adult B eats baby A!

**Second, Polis describes MANY complicated subwebs in the Coachella Desert (southern CA)**

**Polis sells out and lumps, but it's just so that he can test the “assembly rules”**

**Rule**

1. Component chains limited to 3 or 4 links
2. Species only interact with 2-6 other species
3. Omnivores rare (25% of animals)
4. Omnivores feed on adjacent trophic levels
5. Insects and parasitoids are exceptions to 2,3
6. Webs not compartmentalized within habitats
7. Loops not biological reality
8. Lots of top predators (29-47%)

**Polis' Findings**

- NO - He found average of 7 links
- NO - He found range of 10-1000 interacting species!
- NO - He found 75% of animals were omnivores
- NO - trophic levels aren't even a useful concept, given omnivory and especially age structure.
- Yes, but: Exceptions more common than the rules.
- YES - all community members are part of same web
- NO - ontogenetic reversal ; 1300 species cannibalize
- NO - given age structure, it's almost impossible

**Conclusion:**

**Not only were simplified webs very poor descriptors of trophic interactions,**

- they were a poor foundation for general “assembly rules”,
- many of which are simply wrong.

**Power, M. E.** 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* 73:733-746.

[Her answer to question in title is “yes.”] Reviews factors that affect the relative strength of top-down and bottom-up forces in food webs. Reiterates Hunter & Price's (1992) observation that “the removal of higher trophic levels leaves lower levels intact (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all.” Thus, top-down forces may dominate trophic dynamics (as they do in the Fretwell-Oksanen model), but food-web structure is set by the fundamental bottom-up attribute of ecosystems, plant productivity. The general

point of the paper is that t-d and b-u forces are context-dependent. Has two nice food web stories: the Eel River (p. 739) and Rio Frijoles (p. 740).

Main points:

1. Factors that reduce consumer efficiency will weaken top-down relative to bottom-up forces. Predators may not regulate their prey efficiently if they
  - a) fight with each other
  - b) are limited by or compete for resources other than food (eg. shelters, water)
  - c) cause prey to hide or become better defended or if time lags occur between prey consumption and the predator's reproductive response.

Ratio-dependent models take these factors into account.

2. Nonlinear relationships between grazing pressure and plant removal could decouple and destabilize top-down control.  
At low grazing pressures, plant losses may be offset by growth stimulated by recycling of nutrients (released by grazers). As grazing increases, the growth stimulus cannot compensate for the grazing and productivity goes down. Thus, the system is likely to be nonlinear.
3. Feedbacks between non-adjacent trophic levels could affect the balance of top-down vs. bottom-up control. e.g., predator-prey interactions change with the availability of cover and plants, as they accumulate, provide cover. Such dynamic feedbacks could be important but have not been formally incorporated into food-web theory.
4. There are 4 practical issues that need to be resolved before t-d vs. b-u can be tested in nature. They center on the problems of measuring the independent and dependent variables of models (primary productivity and trophic level biomass, respectively, in the Fretwell-Oksanen model) in the field.
  - a) it is difficult to position food webs along productivity gradients. How do you measure primary productivity? What do you do when grazing increases primary productivity?
  - b) Omnivory makes it difficult to distinguish trophic levels, which makes it difficult to measure biomass of trophic levels. Even so, Power thinks that the chain-like, rather than web-like responses to perturbation shown in many aquatic webs (ATC's) demonstrate that even highly complex systems can show top-down control. She suggests that trophic levels should be operationally defined as "functionally significant" if perturbation of them increases densities of organisms one level below. Thus, a web in which all producers and consumers are resource-limited (total bottom-up control) would be classified as having 1 functional trophic level.
  - c) Disturbance and seasonal changes affect biomasses and make it difficult to decide when to evaluate communities.

"Following seasonal or aseasonal disturbances, how long is long enough to assume that all trophic levels that can be supported by the local ecosystem have in fact arrived?"

Eel river example: in a year of low algae productivity, no ATC was observed; but in a year of high algal productivity, an ATC was observed. Thus "plants have primacy in determining the directionality of forces in food webs."

- d) Communities are difficult to circumscribe.

Anticipates the "subsidy" problem championed by Polis and Strong:

"consumers whose population densities are not constrained by the low productivity of barren patches will nonetheless supplement top-down forces within them."

Empirical support for t-d vs. b-u? Consumer and resource abundances are often positively correlated, which suggests bottom-up control. However, the critical test for top-down control is whether resources and consumer

densities remain uncorrelated if productivity varies, but the no. of trophic levels remains fixed. This requires extensive experimentation.

**Regal, Philip. 1977.** Ecology and Evolution of Flowering Plant Dominance. *Science* 196: 622-626

**One sentence summary:** The radiation of angiosperms was connected to the appearance of birds and mammals as seed dispersers, which *then* favored insect pollination.

The appearance of birds and mammals increased seed dispersal far beyond what wind and reptiles (if they were involved at all) could do.

Once trees (he focuses on trees) reach far-away sites, insect pollination becomes favored over wind pollination because it's more efficient over distances and when individuals are sparse.

Biotic pollinators and dispersers open the way for lots of diversification and coevolution.

The importance of mammals/birds explains why angiosperms didn't radiate with insect diversification, but radiated when mammals/birds appeared.

Angiosperm domination:

Angiosperms could invade into gymnosperm areas, and still enjoy outcrossing.

The more this happened, the sparser the gymnosperms became, and their wind-pollination decreased in effectiveness.

Angiosperms didn't out-compete gymnosperms in places where disturbance/harsh conditions prevailed: montane/northern areas, fire-prone areas, barrens.

**Rejmanek, M. 1996.** Species Richness and Resistance to Invasions In: *Biodiversity and Ecosystem Processes in Tropical Forests* Orians, Dirzo, Cushman, eds.

**One sentence summary (or so):** There is a trend for communities to be more invulnerable further from the equator. This trend does not apply to islands, which are about equally invulnerable in tropics and non-tropics. Still hard to know what determines invulnerability – disturbance seems key.

The trends summarized from the literature:

Alien plant species in tropical vs. non-tropical mainlands:

More native species around equator.

More alien species around temperate latitudes.

Alien species on tropical vs. non-tropical islands:

About the same number of alien species on equatorial and temperate islands.

More invaders on species-rich islands.

More invaders farther from the mainland.

Alien species in intact vs. disturbed tropics:

Way more invaders in disturbed areas; very few in intact tropics.

Possible explanations for all these patterns?

High species diversity itself doesn't confer resistance to invasion.

(look at S. Africa and Australia: very rich, very invaded)

Species richness may indicate "favorable conditions," but only invulnerable when there's disturbance

**Rey, Jorge 1984.** Experimental tests of island biogeography theory In: *Ecological Communities: Conceptual Issues and the Evidence*, Strong, Simberloff, Abele, Thistle, eds.

**One sentence summary:** By experimentally removing all the arthropods on small cordgrass islands and monitoring recolonization, Rey's results are similar to the predictions of the MacArthur-Wilson Island Biogeography model. Deviations included 1) less-than-homogeneous extinction rates for all species, and 2) no effect of distance from mainland on immigration rates and species richness.

Species-Area relationships:

The islands showed strong species-area relationships before insect fumigation, and the numbers of species rose and stabilized again to pre-fumigation levels in 20 weeks.

Dynamic Equilibrium:

20 weeks after fumigation, the islands showed stabilization of colonization / extinction rates. However, all species did not have homogeneous extinction rates. The deviation was somewhere between MacArthur-Wilson homogeneity and what would be expected if species had strict successional roles.

Isolation:

MacArthur Wilson predictions were **not** supported here. There was no relationship between species richness, or immigration rates, and distance from mainland/nearest large island.

**Rohde, K., M. Heap, and D. Heap.** 1993. Rapoport's Rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *American Naturalist* 142: 1-16.

**One-sentence summary:** Stevens' (1989) attempt to explain the latitudinal diversity gradient may be statistically flawed and acceptance of it is premature. In any case, the hypothesis that environmental tolerances are narrower in tropical species cannot explain the pattern of diversity in marine teleost fishes.

Stevens (1989) found that species which occur at high latitudes tend to have broader latitudinal ranges. The authors of this paper point out that such a correlation may be an artifact rather than a real biological phenomenon: since the temperate zones are species-poor, a few very wide-ranging species which have the center of their ranges in the tropics can strongly bias the correlation, making it appear that high-latitude species have broader environmental tolerances when they actually do not. The authors suggest a different method for examining the correlation between range breadth and latitudinal occurrence of species. They also note that marine teleost fishes which occur in the tropics have broader latitudinal ranges than those occurring at high latitudes; this is the reverse of the pattern predicted by Stevens (1989), indicating that environmental tolerances of tropical teleost fishes may in fact not be narrower than those of similar, temperate fishes. Both of these observations tend to undermine Stevens' hypothesis. The authors also note that data are lacking for latitudes lower than about 30 degrees N. The generality of the patterns observed by Stevens has therefore certainly not been shown.

**Rosenzweig, M.L.** 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.

**The main point:** depending on the position of the predator isocline in relation to the prey isocline, the equilibrium will either be a steady state or unstable. The "paradox of enrichment" refers to the idea that increasing the limiting resource destroys the steady state, by shifting the predator isocline from the left to the right of the hump in the prey isocline.

Rosenzweig looked at six models of predator prey interactions where predators compete only by depleting each other's resource supply.

The reasoning is as follows: if the predator is proficient at reproducing in the presence of few prey, the system won't persist (the equilibrium is to the left of the hump). If the prey are relatively proficient at escape or the predators are

inefficient (the equilibrium is to the right of the hump), then the system will persist. Let  $P^*$  indicate the peak of the prey isocline. When the predator isocline is to the left of  $P^*$ , the system is unstable. When the predator isocline is to the right of  $P^*$ , the equilibrium is a steady state. If we start with a stable system, enrichment means that  $V^*$  moves to the right, thereby shifting the position of the equilibrium from steady to unstable.

**Schall, J.J., and E.R. Pianka.** 1978. Geographical trends in numbers of species. *Science* 201(4357): 679-686.

**One-sentence summary:** Community assembly in the continental US and Australia. The authors suggest that the basic design of some taxa predisposes them to success and diversification in certain environments, but that communities will by no means converge on the same final state.

This paper examines geographical trends in species richness for terrestrial vertebrate groups of North America and Australia. The authors divided the continental United States and the continent of Australia into quadrats and superimposed on these the species richnesses of amphibians, reptiles, land birds, and mammals, as well as climatic statistics.

The upshot is that environmental conditions have a role in determining the diversity of taxa, but that other factors are also important. In other words, there is a *limited* degree of “community convergence”. For example, the basic lizard design is predisposed to be successful in deserts, while the basic bird design is not. Therefore, lizards are more speciose than birds in deserts on both landmasses. However, historical factors and competition at higher taxonomic levels also influence community composition; for example, the roles played by desert mammals in North America are generally occupied by lizards in Australia. Schall and Pianka note that both direct competition between taxa and opposite correlations with the same environmental variable produce the same patterns of diversity. In other words, if the diversities of two taxa are negatively correlated with one another, it may be because those taxa are competing, but it may also be because those two taxa are responding differently to an underlying environmental factor.

In summary, Schall and Pianka seem to attack three questions. 1) Are diversity trends of given taxa the same across continents? Answer: Not always, implying that we should examine these trends in independently evolved faunas before trying to come up with an evolutionary explanation for them. For example, there has been recent rumbling that the latitudinal gradient in diversity may not really exist in the Southern Hemisphere; this would affect our attempts to explain this gradient! 2) Does taxonomic complementarity (negative correlation between the diversities of two taxa) imply competition between those taxa? Answer: Not necessarily; it’s possible that both taxa are just responding differently to the same abiotic variables. 3) Do communities converge in similar but geographically distinct environments? Answer: Not really; there’s a tendency for certain taxa to succeed and diversify in certain environments, but historical factors are also very important.

**Schindler, D.W.** 1977. Evolution of phosphorus limitation in lakes. *Science* 195: 260-262.

**One-sentence summary:** Complex biological mechanisms exist which make up for nitrogen and carbon deficiencies in freshwater phytoplankton communities; the result is that phosphorus is almost always the limiting nutrient.

Despite the fact that small-scale laboratory experiments indicate that carbon or nitrogen should be limiting nutrients for phytoplankton in some lakes, a series of whole-lake experiments show that phosphorus is actually the limiting nutrient in almost all cases. The reason for the discrepancy is that complex processes which cannot be simulated in laboratory bioassays (e.g. fixation of atmospheric nitrogen, or turbulence which introduces gaseous carbon dioxide) compensate for deficiencies of carbon and nitrogen in nature. Schindler suggests that phosphorus (for which there exists no compensating mechanism) will be the limiting nutrient except in cases where the lake is receiving huge phosphorus inputs or where it has recently experienced a large phosphorus input and has not yet reached an equilibrium.

**Schoener, T. W.,** 1989. The ecological niche. In Cherrett, J. M., *Ecological Concepts*, Blackwell, pp. 79-

113.

The main point in one sentence: A major distinction between earlier (e.g., Grinnell, Elton) and later (e.g., Hutchinson, MacArthur, Levins) notions of ecological niche is that the former regard niches as having a reality separable from their occupants, whereas the latter do not.

The first and longer part of this article presents Schoener's version of how the notion of ecological niche developed from the early 1900s to the present, emphasizing the notions of Grinnell, Elton, and Hutchinson and the hypervolume utilization distribution notion developed from Hutchinson's notion by MacArthur, Levins, and many others. Schoener's pace is leisurely, and he makes plenty of points that I will not rehearse. His main point is that a major distinction between earlier and later niche notions is that the former regard niches as having a reality separable from their occupants, whereas the latter do not. Schoener thinks that some textbooks exaggerate the difference between the influential notions of Grinnell and Elton, both of whom, he argues, thought of a niche as an opportunity for a way of life, involving certain modes of feeding, nesting, and avoiding predation, among other things. Roughly the same niche thus might exist in different locales and be filled by different species, though both Grinnell and Elton acknowledged that the concept would break down if pushed too hard, i.e., that no two species have exactly the same niche. It seems to me that, further developments among ecologists notwithstanding, this general idea of niche remains dominant among educated non-ecologists, e.g., in evolutionary biology textbook discussions of convergence between Australian marsupials and American placentals. In contrast, in Hutchinson's hypervolume notion and the utilization distribution notion developed from it, the occupants are primary, and the niche does not formally exist apart from them. According to Schoener, "This shift to the occupant may have been forced for consistency's sake; Hutchinson, much more than previous workers, imagined niche properties of occupants as readily mutable...If competition between species commonly caused their niches to change, then observation of an occupant's characteristics cannot be used in any simple way to determine characteristics of the 'recess', as would be perfectly possible in Grinnell's concept." (p. 90) Because of both its change of emphasis and its precision of formulation, Schoener calls Hutchinson's notion "revolutionary", and I suppose that from a niche theorist's perspective, it was.

The second and shorter part of this article presents a précis of modern niche theory as of 1989, along with applications, tests, and criticisms of same. Schoener's discussion of the relation of competition to niche overlap is especially interesting. Are competition and niche overlap positively correlated? Most niche-theoretic models suppose so, but some empirical evidence contradicts them. "To lead us out of this tangle," Schoener says, "I have constructed a dichotomous decision tree...Decisions are needed at three levels. First, does or did competition occur? If competition is not an issue, the degree of niche overlap is not specified by niche theory; it will be high if all species are concentrating on the same superabundant food resources. Second, is competition present or past? Past competition has cause niche separation and/or fixed it evolutionarily, so that strong resource partitioning implies minimal present competition: one finds little disease once the patient is cured. Third, given present competition, are the relevant niche dimensions fine- or coarse-grained? If the former, we have ordinary niche theory, which assume consumers and resources are in a well-stirred soup. Here, the greater the overlap, the greater the competition. If the latter, we have Brew's (1984) model in which lower overlap is associated with greater competition." (pp. 104-5, most references suppressed) After analyzing a couple of examples from this perspective, Schoener concludes, "Thus it seems there is nothing wrong with the logic of the theory, but the decision tree requires rather detailed information." (p. 105)

**Schwartz and Hoeksema.** 1998. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology*: in press.

A two-species, two-resource graphical model.

Main points:

- 1) Both individuals realize an advantage through trade if they trade at a trade cost ratio (T) somewhere in between their respective isolation cost ratios (I). Thus if the tree has an I of 1:1 (P and C are equally easy to get) and the mycorrhizae has an I of 3:1 (per unit effort, it can get 3X the amount of P compared with C), they will both

benefit at a T of 2:1.

- 2) The gain (G) (which is the increase in resource acquisition with trade, compared to not trading) is greater for a species the more similar T is to the I of the other species.
- 3) Even a relatively poor resource competitor benefits from trade if its I is not 1:1 (if it is better at acquiring one resource than the other). Thus, even though the tree in the example is better at extracting both C and P than the mycorrhizae, a mutualism is still profitable for both.
- 4) The model can accommodate shifts in resource availability and predicts when such shifts make trading unprofitable. The relationship then either becomes parasitic or is abandoned depending on the abilities of the species involved to terminate. This corresponds well with Bronstein's observation that most mutualisms that have been adequately investigated are conditional.
- 5) Under this model, mutualisms can get started without costs to either partner. Is this equal to the (by-product, by-product) basal mutualism of Connor 1995?

Ken's ideas:

- works well when resource 1 and 2 are similar (common currencies)
- hard to apply to services (what does the consumption vector become? are services consumed?)
- hard to apply to obligate mutualisms (how can you anchor the isolation acquisition isocline when the mutualist can't get one resource in isolation?)

**Shumway & Bertness 1994.** Patch size effects on marsh plant secondary succession mechanisms

**One sentence summary:** size of disturbances interacts with plant life-history traits to give different types of successions. A warning against extrapolating to diff. scales.

Rhode Island. Marsh dominated by *Spartina* (seaward) and *Juncus* (landward). Bare patches are formed when tidal wrack stays in place and smothers vegetation. Solar evaporation increases salinity in bare patches, only *Salicornia* can est. seedlings in any numbers.

In large disturbed patches, salinity is so high that only the salt-tolerant *Salicornia* and *Distichlis* can est., these shade the substrate, lessen solar-induced salinization, and facilitate the est. of *Spartina* and *Juncus*. In small patches, facilitation does not happen, and all species duke it out competitively.

**Sih, A. 1980.** Optimal behavior: can foragers balance two conflicting demands? *Science* 210: 1041-1043.

**The main point:** an experiment confirmed that foragers can balance the need to forage efficiently and the need to avoid predators while feeding.

**The system:** aquatic insect, *N. hoffmanni*. Adults eat young, and both eat flies. Experimentally-created conflict situation in experimental tubs: central region had a high prey density but a high risk of predation. Edge region had low prey density and low risk of predation.

**Methods:** calculated relative fitnesses associated with time spent entirely in one region or the other by constraining foragers to either region and measuring feeding rates (single measure of relative fitness).

**Results:** foragers spend more time in region with higher feeding rates, the greater the relative advantage of a region, the greater the preference for that region.

**Conclusion:** foragers can adaptively balance the conflicting demands of feeding efficiently and avoiding predators.

**Silander, J. A., and S. W. Pacala. 1990.** The application of plant population dynamic models to understanding plant competition. In *Perspectives on Plant Competition*, pp. 67-91. Academic Press.

Brief summary: presents a neighborhood model of plant competition and its application to a 2-species system (old field annuals: pigweed & velvet leaf). Main conclusion: keeping track of the precise neighborhood (species composition and density of neighbors around an individual of the species you are studying) is crucial for accurately modeling population dynamics only in some cases (e.g., when individuals are clumped, and/or neighbor density is

low or variable).

Introduction: Silander & Pacala review the characteristics of several plant models.

Model	Type	Spatial?	Analytically tractable?	Has Density Dependence?
Tilman	mechanistic	N	N?	Y
Shugart	mechanistic	N	N	Y
Silander & Pacala	phenom	Y	sometimes	Y
Leslie matrix	phenom	N	Y	N

Model structure: the main variable is the population density of seeds of the target species produced in year  $t$ . This is determined by 4 submodels. The competitive dynamics in submodels 2 & 3 are determined by the number of conspecific and heterospecific neighbors enclosed within a series of concentric circles around each individual of the target species, and by the coefficients of interference as measured in the field.

- 1) germination submodel: gives probability that seed produced in year  $t$  will survive to and germinate in year  $k$
- 2) survivorship submodel: gives probability that a seedling will survive to adulthood, based on neighborhood densities
- 3) fecundity submodel: gives the number of seeds produced by an individual, which is based on its size, which in turn is based on its neighborhood density
- 4) dispersal submodel: predicts the spatial location of dispersed seeds given the parent location.

The basic conclusions:

- 1) Neighborhood models can closely predict the population dynamics of simple communities (1 or 2 species). More diverse communities are too hard to parameterize (that is, its too hard to do the field experiments to measure the parameters).
- 2) In some cases (as in the pigweed/velvet leaf system modeled here), a "collapsed" model that uses mean densities of neighbors instead of keeping track of neighbors specifically works just as well as the full model. "Collapsed" models are likely to work for species in which densities of neighbors are high with low variance, and the target species is distributed randomly or is overdispersed. When densities of neighbors are low or variable, or when the target species occurs in clumps, the full model is likely necessary. "Collapsed" models can be analyzed analytically, while full models cannot.
- 3) Dispersal is a key component; different dispersal distances can radically change model outcomes. In some cases, dispersal is as important as the relative magnitudes of intra- and interspecific interference in determining the outcome of competition (exclusion or coexistence).

**Sjogren, P.** 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biol Journal of the Linnean Soc* 42: 135-147. (Also reprinted in Gilpin & Hanski?).

**The main point:** the rescue effect (immigration) may save some populations within a metapopulation from extinction.

**The system:** 60 local populations of pool frogs along the Baltic coast in Sweden. Classified these local populations as either 1. extinct; 2. frogs present but no reproduction; 3. reproducing population.

**Methods and Results:** Measured the probability of extinction relative to distance from a neighboring population and found that extinction probability increased with interpopulation distance. Wanted to determine the relative effects of demographic stochasticity and inbreeding in determining local extinction. He measured inbreeding depression by an indirect measure (proportion fertilized eggs) and found that populations further away were not more likely to be inbred. He thus concluded that demographic stochasticity was probably responsible for local extinction.

**Implications:** immigration and colonization rates decrease with increased isolation in patches, while extinction probabilities increase along the same gradient, thus immigration may affect local extinction by the "rescue effect". This paper offers support for this. Don seemed more interested in this result than in the demographic versus inbreeding cause of extinction result.

**Slobodkin, Smith, Hairston.** 1967. Regulation in terrestrial ecosystems, and the implied balance of nature.

A response to Murdoch and Erlich & Birch. Still has wishy-washy definitions.

In response to Murdoch's point that plants may be inedible, says "all green plants are edible. Within every native environment of every species, several herbivores can be found that are capable of extensive injury."

Apologize for lumping in the pollenivores and granivores; says they are not part of the herbivore trophic level; thus HSS still stands.

They detail several ways in which HSS may be disproved (in response to Murdoch); but these tests STILL contain weasel words like "the major part," "dominant," "resource-limited" etc. Really are no closer to specifying empirical tests.

**Sousa** 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225-1239.

**One sentence summary:** The first good empirical test of the intermediate disturbance hypothesis (IDH); the IDH is supported. Note that Sousa was Connell's student.

An algal-dominated boulder field in S. California. Winter storm-generated waves turn over boulders, setting the successional clock back to zero. Because different-sized boulders are turned over at different frequencies (large less frequently than small), a mosaic of successional stages coexists. Intermediate-sized boulders have intermediate disturbance rates and the highest local diversity (local = boulder).

\* Small boulders: dominated by the green algae *Ulva* and the barnacle *Chthamalus*

\* Intermed. boulders: *Ulva*, 4 spp. of red algae incl. *Gigartina*, and *Chthamalus*.

\* Large boulders: dominated by the red alga *Gigartina*

The validity of this pattern was tested via experimental cleaning of 32 small boulders. Half were stabilized on wooden frames anchored in the intertidal; the other half (controls) were tagged but left to roll around. Boulders monitored for 2 years. Controls never reached high diversity (had patchy *Ulva* cover) and in fact were wiped clean at the end of the experiment by a storm. Stabilized boulders reached high diversity (as high as large, naturally occurring boulders) which then began to decline towards the end of the experiment as *Gigartina* took over. Thus it is the disturbance regime, rather than the size of the boulder itself, that determines diversity.

The "nonequilibrium" view of community structure comes from the idea that disturbance is required for the maintenance of diversity in this system. Without it, all the early and middle successional species would be eliminated. Equilibrium exists globally, not locally.

**Sousa** 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65:1918-1935.

**One sentence summary:** size and location of disturbance-caused patches has important effects on the path of succession (similar conclusion to Shumway & Bertness' 1994 salt marsh study) and on regional species diversity.

This study was undertaken in the same type of *Mytilus* mussel-dominated intertidal zone that Paine & Levin (1981) and Dayton (1971) studied. Waves and debris smash into the mussel bed, free up a patch, which is colonized by fugitive species (algae and barnacles) which head for local extinction as the competitively-dominant mussels close in. This study focused on algal succession & ignored the barnacles.

Patch size: Small patches are characterized by high grazer pressures, mostly from limpets that inhabit the surrounding mussel matrix (the limpets apparently take refuge there from bird predators, wave action, and desiccation). Thus the assemblage of algae in small patches consists of crustose, often calcified, grazer-resistant (but competitively inferior) species. Larger patches have half the density of limpets, and consist of grazer-intolerant (but competitively superior) algae species. % cover is lower in small compared with large patches.

Patch location: patches located in matrix areas where cover of epizoic algae (growing on mussels) was high were characterized by high percent cover of several algal species, and vice-versa, indicating short-distance dispersal of propagules and local recruitment of algae.

Although the endpoint of succession is not related to these patch size and location considerations (mussels eventually take over), regional species diversity is. If only large patches were created, the grazer-resistant, competitively inferior algal species (which need refuges in the form of small patches) might disappear from the system. Ditto for grazer-intolerant species if only small patches were created.

**Spiller, D. A., and Schoener, T. W., 1996.** Food-web dynamics on some small subtropical islands: effects of top and intermediate predators. In Polis, G. A., and Winemiller, K. O., *Food Webs: Integration of Patterns and Dynamics*, Chapman and Hall, pp. 160-9.

**One sentence summary:** Small islands in the Bahamas host a well-studied trophic system that is superficially four-level but effectively three-level, in that top predators (lizards) eat herbivores (herbivorous arthropods) even more than they eat intermediate predators (web spiders).

The content of this article is largely that of Schoener's March 9 lecture. According to the HSS hypothesis, as elaborated by Oksanen et al., 1981 and many others, in three-level trophic systems, predators promote producers, but in four-level trophic systems, top predators suppress producers; such analyses assume that top predators eat intermediate predators only. On small islands in the Bahamas, there are plants, herbivorous arthropods, web spiders, and, often, lizards. Ignoring whatever eats them, lizards are top predators, but they eat not only web spiders but also herbivorous arthropods. Thus it is interesting to investigate whether lizards promote or repress plants. By means of extensive studies, both observational and experimental, Spiller and Schoener have demonstrated that the net effect of lizards on plants is predominantly positive. When lizards are present, they eat more than enough of most herbivorous arthropods to compensate for their consumption of web spiders; when lizards are absent, the increased predation by web spiders does not fully compensate for the lack of lizards. Thus the trophic system is effectively three-level. Of course, there are exceptions. E.g., there are gall midges that spiders eat but lizards do not, presumably because the midges are too small, hence in one experiment, the presence of lizards was correlated with an increase in galls. It is also interesting that lizard effects on web spiders appear stronger in wetter years, perhaps because the lizards respond numerically to the abundance of herbivorous arthropods in wetter years even more than do the spiders.

**Stevens, George C. 1989.** The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am Nat* 133(2): 240-256.

**One-sentence summary:** At higher latitudes, organisms can tolerate a broader range of climatic conditions; therefore they experience environmental heterogeneity only on a very coarse scale. At low latitudes, organisms are finely adapted to narrow climatic conditions and experience a fine-grained environment. Since organisms "slop over" into nearby habitats, tropical systems become more diverse.

This paper tries to explain the latitudinal diversity gradient (LDG). For most taxa, within-taxon richness increases as one approaches the equator. Stevens' hypothesis is based on what he calls "Rapoport's Rule". This is the positive correlation that supposedly exists between the latitudinal *midpoint* of a organism's geographical range and the latitudinal *breadth* of that range. In other words, high-latitude organisms range broadly north and south.

Stevens argues that, because any given location at high latitudes experiences strong seasonality, “climatic specialists” can’t exist at high latitudes. High-latitude organisms must be adapted to a broad range of climatic conditions; this allows them to spread out to both north and south. Because the tropics experience less variability, the scale of microhabitats is much smaller there (as experienced from an organism’s point of view). This finer mosaic of microhabitats in the tropics supports a mosaic of microhabitat specialists with narrow climatic tolerances.

Stevens hypothesizes that, because the mosaic is fine compared to the dispersal capabilities of the organisms, the organisms are continually flowing out of their specialized “source” habitats into adjacent “sink” habitats, inflating within-habitat diversities. This hypothesis essentially relies on a competition-based theory of community assembly, with competitive exclusion mediated indirectly by climatic effects.

This is a novel and interesting hypothesis. It has gotten a lot of attention recently, but it has what in my mind are some severe flaws. The “Rapoport’s Rule” correlation does not seem to exist for some organisms, and has been questioned by other authors as a general explanation for the LDG. See the rebuttal by Rohde, Heap, and Heap (1993).

**Strauss 1991.** Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology* 72: 543-558.

The effects of whitetail deer, a chrysomelid and a cerambycid on smooth sumac (*Rhus*) and on each other via the plant. Cedar Creek.

- Chrysomelid was most injurious & exerted strongest selective pressure; damage (measured via growth, survivorship & fruit production) was still detectable after 3 yrs. Cerambycids were also injurious. Deer were never injurious and were potentially beneficial.
- effects of herbivores were not additive; both amplifications and cancellations of effects were observed
- interactions existed betw. every herbivore pair; most interactions were temporally separated & therefore were mediated by the sumac. Examples: beetle damage decreased prob. of deer browsing the following year; Chrysomelid damage facilitated later cerambycid oviposition. Point: indirect as well as direct effects on plant fitness.
- in spite of the complicated situation, the selective effects of herbivores were not diffuse, but were consistent from year-to-year over the 3 yr study. Prediction: sumac should allocate to defense against chrysomelids, rather than to a “generalized” defense system against all herbivores.

**Strauss, S.Y.** 1991. Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology* 72: 543-558.

**One-sentence summary:** Herbivory is complicated. Herbivore damage can occur in different ways and the effects can differ in magnitude and direction, as well as interacting with the effects of other herbivores in a highly non-additive fashion.

This paper examined the effects of 1) chrysomelids (flea beetles), 2) cerambycids (long-horned beetles) and 3) deer on sumac (*Rhus glabra*). The interactions within this limited herbivore community are extremely complex, but the main points can be summarized as follows:

1) Different herbivores have different effects in terms of the *type* of attack, the *direction* of its effect on the plant, the *magnitude* of that effect, and the *persistence* of the effect. For example, the two types of beetle attacked different parts of the plant, and had different effects (cerambycids damaged the plant; chrysomelids not only damaged the plant but induced changes in plant architecture). Deer browsing actually appeared to *benefit* sumac. Moreover, while the effects of some damage (that done by chrysomelids) could still be seen two years after the actual attack, the effects of other damage (e.g., deer browse) did not persist longer than a single season.

2) Herbivores can interact directly or indirectly and can affect one another positively or negatively. For example, sumac ramets attacked by chrysomelids were more attractive to cerambycids; conversely, beetle attack made ramets less likely to be browsed by deer. Every member of this limited herbivore community interacted with every other member in some way, with these interactions mostly mediated via the host plant. In none of these cases was the interaction symmetrical. Effects of the various herbivores on sumac were *not* additive.

3) It has been proposed (Fox 1981) that, because plants are attacked by an array of herbivores, they should evolve general defenses. However, over the three years of this study, the selective effect of the herbivores on sumac (due to both direct and indirect effects) remained constant. This suggests that sumac should be under selective pressure to defend against specific herbivores rather than “diffuse” herbivory pressure.

**Strong, D. 1983.** Natural Variability and the Manifold Mechanisms of Ecological Communities *Am Nat* 122(5): 636-660. (Round Table Issue)

**One sentence summary:** There are lots of very common processes that maintain communities *other than competition theory*.

Part I: Logical/Philosophical Points

Hypothesis-testing

The tougher the test, the more assurance we have in its predictions.

Ecology is riddled with weak tests, especially competition theory.

Unambiguous null hypotheses are crucial !!!

Hierarchy of ways to investigate community assembly

Indiv. ecology, not competition, has better, more general explanatory power.

Biogeography explains commun. patters well by treating indiv. ecology and competit. as random in overall effect, but it can't explain mechanisms that generate the predicted patters.

Character displacement & competitive coevolution: evolutionary parts of competition theory

Empirical and theoretical work show they're uncommon at best.

Autecology much more important (several examples).

Part II: Examples of non-competition theory ecology

Herbivorous insects [1/4 of earth's macroscopic species]:

Don't fit resource depletion/niche models, not highly density dependent

Autecology, vertical food web, weather/fire good predictors of community struct.

Decomposer/parasitic insects [1/4 of earth's extant species]:

No hints of competitive influence in decomposers

Examples of competition in parasites has effects contrary to predictions

Plants: autecology primary; cases of competition are much more complex than niche theory can explain

Vertebrates: same deal

Conclusion: Competition theory does very little to explain community assembly. Either autecology, vertical trophic interaction, or environmental effects are more important, or competition is too complex and interactive with other effects for niche theory to explain.

**Strong, D. R. 1983.** Natural variability and the manifold mechanisms of ecological communities. *The American Naturalist*. 122(5):636-660.

**One sentence summary:** The assumption of a singularly overriding force of competition in community ecology, is in error due to the numerous relationships that influence communities.

This essay (not really a review) is a broad explanation of why assumptions of single large effect forces that structure communities are not useful. Communities are complex assemblages and as such have complex sets of dynamics that work in concert to create the community structure.

Philosophical points:

- Hard tests and falsifiability are key in scientific progress. Competition models that have been proposed lack a

null hypothesis. The lack of a null hypothesis cannot be used as means of support for competition.

Individualism (autecology) is viewed as the perspective that is between the two extremes of competitionism and the idea of the super organism.

- Community stochasticity is defined as assemblages with no tendency of persistence or resilience. This implies at least one variable in the system has a non-zero variance. It is generally impossible to distinguish deterministic chaos from stochastic behavior.
- Niche theory is at best a concept due to its lack of predictions and falsifiability.
- Character displacement / coevolution are extreme extensions of competition theory. No empirical evidence for character displacement. Competition fails to explain morphological differences (usually it is explained by variation in diet).

Density Vague Populations:

- The definition of density vague is a population with low correlations between population parameters and density. This does not imply no relation between these variables.
- Examples include herbivorous insects, barnacles, and some fish.
- Herbivorous and decomposer insects do not have dynamics explained by competition theory or niche theory.
- Invertebrate parasites occupy only a small percentage of available niches. In this environment niche theory does not seem to operate and there is little need for competition.
- Plant studies appear to support non-equilibrium dynamics and do not support niche or competition theories.

**Strong, D.R.** 1997. Quick indirect interactions in intertidal food webs. *TREE* 12(5): 173-174.

**One-sentence summary:** Researchers have been afraid that indirect interactions in food webs (one species affecting another via a third species) are too intractable to study, but Strong reviews an article by B.A. Menge and concludes that indirect effects are not as subtle or delayed as people have feared.

This is a review of a paper (Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Monogr.* 65: 21-74) which is itself a review of a number of papers on intertidal trophic interactions. "Indirect interactions" are a type of interaction in food-web studies in which influences between two species are changed by interactions between other species. For example, exploitation competition between two predator species is an indirect interaction: the two species may never interact directly, but by interacting mutually with a third species, the prey, they do indirectly affect one another.

Menge apparently found indirect effects to be quite strong and pervasive, nearly as strong and pervasive as direct interactions. Some observers of food-web theory have worried that indirect effects, being more inobvious, intricate, or (especially) delayed, could be the monkey's wrench in the enterprise. The problem is that, if indirect effects are subtle or show up only after a long lag time, understanding food webs which include indirect effects would require very long-term research and better knowledge of natural history than we have now. However, Menge found that both direct and indirect effects appeared quite rapidly in most studies, refuting this pessimism. Apparently the current methods and natural history are at least up to starting the job, and work in the intertidal seems to show that indirect effects are not intractable bogeys to be feared. Strong ends by calling for an extension of the sort of work done in the intertidal to more complex terrestrial habitats, as well as to soil organisms and detritus-based food webs (no surprises there). He also exhorts researchers, based on Menge's findings, to tackle questions of indirect effects in food webs without fear.

**Strong, D.R., McCoy, E.D. & Rey, J.R.** 1977. Time and the number of herbivore species: the pests of sugarcane. *Ecology* 58: 167-175.

**The main point:** host geographic range (area), not time, better explains herbivore diversity. Anti-time hypothesis to explain species richness.

**The system:** sugarcane and their pests. Sugarcane was introduced around the world at various times, ranging from 1000BC to the 1800s. There are excellent records on sugarcane and the diversity of their pests. Thus this study differs from others which have relied upon indirect estimate of age.

**Methods and Results:** used dates of sugarcane introductions around the world to detect influence of host age upon associated pest richness. Regression analysis with age as independent variable. Area was by far the best predictor of pest richness (they also looked at time and latitude, neither of which was significant).

**Interesting stuff:** sugarcane pests are highly endemic! "Of the 1645 known sugarcane pest species, 959 occur only in a single region and 156 only in two regions." They interpret this to mean that pest-species accumulation is rapidly asymptotic, the limit determined by the hosts' geographic range. This interpretation is in line with other results which have shown that beyond an initial few hundred years, younger host populations have the same number of pests as older host populations. These results also seem to suggest that areas may become saturated, contra the time hypothesis, which predicts that species should continue accumulating through time, and their numbers shouldn't asymptote. ??Don seems to think that the rapid proliferation of insect species shows that interspecific competition isn't important and thus contradicts niche assembly theory (Sanders), although I find that interpretation questionable.??

### Tilman 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients.

Seven gradients established by adding N at Cedar Creek (3 fields of diff. ages X existing vegetation left vs. plowed = 6 gradients, plus one existing vegetation gradient in oak savanna).

- 1) in high-N treatments, diversity decreased significantly and consistently across habitats (60% of spp. disappeared by year 5). Suggested mechanisms: nutrient addition makes plots more homogeneous spatially, forcing more species to compete for the same limiting resource. [Consistent with paradox of enrichment!]
- 2) these experiments (and a survey of 22 old fields) lead to the conclusion that N supply rates are a primary determinant of succession in Cedar Creek old fields
  - a) N increases during succession
  - b) species that came to dominate high-N parts of gradients were characteristic of late successional habitats.
  - c) outcome of interspecific interactions depends on N supply rates
- 3) Species had individualistic responses to N: normal curves in most cases ([N] on x-axis, % cover on Y)
- 4) Successional endpoints (after 5 years) of the different habitats were independent of initial plant abundances; species composition converged despite great differences in initial species composition. "multiple stable equilibria... cannot be demonstrated in these old-field communities."

### Tilman and Pacala. 1993. The maintenance of species richness in plant communities. In Ricklefs & Schluter, *Species Diversity in Ecological Communities*.

Starts out by asking "why are there so many species out there?", when the basic model (homogeneous, equilibrial habitat) predicts few species. Turns out that any violation (e.g., spatial or temporal heterogeneity) allows a potentially unlimited number of species (they go through numerous models here). So they rephrase the question, "why are there a particular number of species, and not many, many more?"

#### I. Processes allowing persistence of numerous species

$R^*$ : the resource concentration at which the resource-dependent growth rate of a species exactly balances its total loss rate from herbivory, senescence, mortality, and all other sources of biomass or nutrient loss. [Tilman seems to assume that each species can reduce the resource to that level] The species with the lowest  $R^*$  for a particular resource will competitively exclude all other species where that resource is the most limiting (assuming: homogeneous habitat, at equilibrium, with no limiting physical factor, no neighborhood effects, no habitat patchiness, only two trophic levels = resource and consumer with no pests, simple life histories.) It does so by reducing the resource down to a level at which only it can survive. The number of species that can stably coexist in a homogeneous, equilibrial habitat is less than or equal to the number of limiting resources plus the number of constraining physical factors.

The idea of the tradeoff is crucial; no species can be good at everything, otherwise diversity would always be low. E.g. an *Andropogon* at Cedar Creek is one of the best competitors for N because of its 70-85% allocation to root, but a poor colonizer because of low allocation to seed and rhizome. This is the classic "competitors vs. colonizers" dichotomy. Another classic: tradeoff between competitive ability and susceptibility to predation.

Neighborhood effects: "because of local resource use, even fine-scale intraspecific clumping serves to increase the strength of interspecific competition relative to interspecific competition. General models, such as the Lotka-Volterra model, predict that coexistence becomes more likely as between-spp. competition becomes weaker relative to within-species competition." [Nice tie in with Wills. et al. 1997's density-dependence].

## II. Processes that limit diversity

Small pop. size - random walk to extinction for rare species. Fluctuations in environment can reduce pop. sizes, increase extinctions, and limit diversity.

## III. Patterns in diversity

1) Spatial heterogeneity and organism size: May suggested that habitat heterogeneity is fractal, and the smaller the organism, the more heterogeneous the environment, and the higher the possible diversity. Thus the fact that smaller animals are more diverse.

2) Productivity gradients: the hump-shaped pattern. As productivity increases, individual plants get larger. possible explanations for the hump-shaped pattern:

- As plants get larger, resources become more uniform because each plant has a larger foraging area. This reduces spatial heterogeneity & may reduce diversity (drop off after hump).

- As plants get larger, light becomes the limiting resource. Tilman uses graphical models I don't understand to say that this produces the hump shape.

- As productivity increases, individual plants get larger and populations sizes get smaller. The random walk to extinction for small pop sizes may explain the drop off in diversity.

- Denslow 1980: more spp. should be adapted to deal with the most common habitat conditions than with other conditions. Intermediate productivity is the most common scenario (no citations), thus most species do best at intermediate productivity, thus hump shape.

3) Disturbance gradients: another hump-shaped pattern

Cites Levin and Paine (1974) for the intermediate disturbance hypothesis.

4) Latitudinal gradients: This is another hump-shaped pattern !!! although Tilman does not make this point possible explanations:

- species-energy theory [a variant of productivity gradient above]: more productive habitats (e.g. the tropics) allow higher pop. densities which reduce random walks to extinction & increase diversity. This may work for birds, etc., but does not work for plants: larger individuals and lower pop densities mentioned above.

- a variant of the intermed. dist hypothesis: the poles have variable weather & glaciation (= high disturbance) causing high extinction rates (originally suggested by Wallace 1878). Tropics have intermediate dist rates.

**Tilman, D.** 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. In *Perspectives on plant competition* (ed. J. Grace and D.E. Tilman), pp. 117-141. NY:

Academic Press.

**One-sentence summary:** Tilman proposes the  $R^*$  mechanism of plant competition: the species which can survive on the lowest concentration of the locally limiting nutrient draws the level down to that concentration, displacing its competitors.

Tilman bemoans the fact that studies of plant competition have been descriptive rather than mechanistic and proposes  $R^*$  as an antidote to the problem. He suggests that 1) competition can be best studied by looking at how each species interacts with its resources (we're assuming exploitation competition rather than interference competition here), and 2) all organisms are constrained by tradeoffs, e.g. a good competitor for light cannot simultaneously be a good competitor for nitrogen. Tilman proposes a series of models, from a very abstract simple one to a more realistic complex one. All of them hinge on some incarnation of  $R^*$ , which is defined as the concentration of the locally limiting nutrient which a species needs to survive. At *equilibrium*, the species with the lowest  $R^*$  will increase in numbers, drawing down the concentration of that limiting resource. As this concentration falls, species with higher  $R^*$ 's will be displaced from the community, until only the species with the lowest  $R^*$  is left. Because of the inherent tradeoffs in plant traits, Tilman predicts that species will be just as efficient or fast-growing as they need to be in order to survive.

**Tilman, D., 1990.** Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58:3-15.

**One-sentence summary:** Blessed are those who discern and model environmental constraints and organismal tradeoffs, for they shall be enlightened (for details, see Keddy, 1991).

This article is an expanded version of a lecture, and it reads something like a sermon, preaching the gospel according to Tilman. Here's a sample: "The simplicity we will find in ecology...will come from an overlying mechanistic framework that allows us to determine the cause of a given pattern. For almost all ecological patterns, this framework is provided by the concept of environmental constraints and organismal tradeoffs." (p. 11) Like any evangelist, Tilman repeats the point enough that nobody could miss it, and he offers glowing testimonials. These are interesting. However, they were all reviewed by Keddy, 1991, as summarized by Whitney, so I'll keep it short here.

Tilman's first case studies are experiments measuring  $R^*$  for soil nitrogen, i.e., asymptotic abundance of soil nitrogen for monocultures growing in nitrogen-poor soil, for five grass species, along with experiments showing the winner of pairwise contests among these species is consistently the species with the lower  $R^*$ . Here, low nitrogen is an environmental constraint, and low  $R^*$  is correlated with high root biomass, which is interpreted as a favored resolution of an organismal tradeoff, in that root biomass is more valuable than shoot, leaf, or other biomass for competitive success under this environmental constraint.

Tilman's second case studies are observations and experiments on succession, involving both the grasses and other plants. These support the hypothesis that early successional grasses are good colonists but poor competitors due to allocating resources more to seeds and less to roots, while late successional grasses are the opposite. Later still, soil nitrogen rises, nitrogen competition becomes less significant, light competition becomes more significant, and superior light competitors take over, turning prairie grassland into oak woodland. Here, both soil nitrogen and light are limiting resources, but at different times, so that different resolutions of the organismal tradeoff between root biomass and shoot or leaf biomass are preferred at different times.

**Urban and Shugart 1992.** Individual-based models of forest succession.

Describes "gap models," a class of models derived from Botkin's (1972) JABOWA model. FORET was a major offspring which eventually gave rise to ZELIG. Gap models simulate the establishment, annual diameter growth, and mortality of each tree on plots of 100-100m<sup>2</sup> (which correspond roughly to an adult tree's canopy and "zone of influence"). Models can be parameterized for several species and are thus good for mixed-species, mixed-age forests. Not usu. spatially explicit although some extensions have been developed. Usu. used for northern

hardwood forests.

Tree height, leaf area, and biomass are calculated allometrically from diameter. These factors determine competition which works through a tree > plot > tree loop. Each tree shades all shorter trees in the plot, and is shaded by all taller trees. Demographic processes (establishment, growth, mortality) are modeled by taking the optimal behavior and reducing this optimum to reflect the environment defined in terms of

- 1) available light [considered THE most important constraint]
- 2) soil moisture
- 3) soil fertility
- 4) temperature.

Growth is based on logistic curve. Establishment is stochastic and ignores dispersal, germination, and early survival; individuals of species tolerant of the current environmental constraints survive (implicitly assumes all species are available to establish). Mortality is treated probabilistically with a background annual mortality of 1-2% and further mortality imposed when growth has been poor (loss of vigor). Feedbacks vary with models, but in most trees influence light and soil nutrients but not soil moisture or temperature.

Applications of gap models:

- 1) shifting mosaic steady-state  
Encapsulates Bormann and Likens (1979) view. Mosaic of plots in four stages of succession: reorganization (incl. establishment), aggradation, canopy breakup, and the steady state. On the plot level, the dynamics are non-equilibrium (trajectory zooms all over the principal components plot where axis I = abundance of small trees and axis II = abundance of large trees). However, on the stand (all plots together) level, dynamics are a smooth spiral trajectory into an equilibrium point.
- 2) Forest habitat dynamics and avian succession  
Defined microhabitat variety in terms of statistical variance in principal component scores, and graphed the trend in microhabitat variety during succession. Microhabitat diversity rises, peaks, and falls during succession, as does bird species richness. "Supported by empirical studies" (whatever).
- 3) Life-history traits and succession  
Huston and Smith (1987). Constructed hypothetical tree species in terms of 5 traits: max. size, longevity, max growth rate, shade tolerance, and sapling establishment rate. Then for pairs of species differing in only one of these traits, they ran the model. Found that all species pairs fit one of 5 successional pathways (a small subset of the possible patterns?!): classic successional replacement (one dominates, then disappears as the other takes over) divergence (both establish, but one eventually takes over) convergence (coexistence at equal abundances) total suppression (one takes over very quickly, other never really establishes) pseudocyclic replacement (trade dominance back and forth in cyclic fashion) \*\* showed that a single mechanism, competition for light, could result in a variety of successional pathways, depending on which life-history strategies were represented at a site.
- 4) Forest dynamics and ecosystem function  
Incorporate feedbacks between nutrient content of litter, litter decomposition, and subsequent establishment. Pastor and Post (1995, 1996) modeled pines (favored on poor, xeric soils) and maples (favored on fertile, mesic sites). Pines have low-quality, and maples high-quality, litter. "Divergent pathways": if the soil starts poor, pines establish and continue to dominate; if the soil is moderate or good, maples establish and amplify their dominance by building the soil.

Shugart's 4 "functional roles": regenerates in gap (yes/no), mortality creates gap (yes/no). Two-level competition: species compete within roles, but roles also compete against each other: any role-1 species that is successful favors all other role-1 species in the next generation. Species within roles are "functionally redundant... interchangeable cogs in the machine" (reminiscent of Hubbell 1997!).

[All these applications make me think that any story we want to tell ourselves about succession can be proved "possible" by a model].

**van der Meijden et al. 1988.** Defense and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51: 355-363.

SYS says: this is one of the first papers recognizing that tolerance (=regrowth) is a major strategy used by plants to deal with herbivory (defensive compounds had previously occupied everybody's attention). However the data presented is not that convincing.

Plant species differ strikingly in the intensity of defoliation. "The hypothesis is formulated that defense mechanisms and regrowth capacity are alternatives. Given a limited amount of energy and nutrients available in the struggle against herbivores, there should be a tradeoff between these two mechanisms." Regrowth capacity comes from "allocation of reserves to those parts of plants [e.g. tubers & roots] that are relatively free from herbivore attack; these reserves can be reallocated after herbivory." We expect a + correlation between amount of herbivory and regrowth capacity; thus a measure of regrowth capacity is the reciprocal of herbivory amount.

Five species of dune biennials were studied. Survival was similar across species despite widely varying amounts of herbivory, providing evidence that some sort of tolerance mechanism is operating. The prediction that herbivory and regrowth should be + correlated is supported: when the 5 spp. were listed in rank order, the most damaged one showed the most regrowth, etc. However, the prediction that the root-shoot ratio is + correlated with regrowth was less supported (it's difficult to tell because r values for the correlations are not given!).

**Walker & Chapin 1987.** Interactions among processes controlling successional change.

A response to Connell & Slatyer 1977. The 3 C&S models are valuable, but they mix together a large number of components ("successional processes") into only 3 recipes and so do not always apply. Many successional processes occur simultaneously and therefore cannot always be grouped into alternative models.

E.G., the Alaskan primary succession from alder -> spruce. Alder adds N, facilitating spruce growth; however, alder litter inhibits spruce seed germination and establishment, and the thick alder canopy inhibits spruce seedling growth. The net effect was inhibitory. This example does not fit into any of the 3 C&S models.

Often, life history traits (propagule arrival and establishment, growth, and longevity) are sufficient to explain successional change without the need for any biotic interaction. This does not fit any C&S model either, all of which have an interaction component (usu. competition). Biological interactions may be more imp. in rate rather than endpoint.

"Succession is a continuum from early stages where factors governing colonization are most important, to late stages where factors governing senescence and mortality predominate." Set of graphs that show the "relative importance for species change" of different factors (e.g. competition, mycorrhizae) as you move through colonization, maturation, and senescence stages.

**Weis & Abrahamson. 1985.** Potential selective pressures by parasitoids on a plant-herbivore interaction. *Ecology* 66:1261-1269.

Main point: a third trophic level can significantly affect evolution of a plant-herbivore relationship.

A gall-making fly, a tall goldenrod, and a parasitoid wasp. The fly larvae induces the gall; the wasp oviposits into the gall and kills the fly larvae. Galls attacked by wasps are significantly smaller than galls in which the fly survives. This could be caused by one of two scenarios, leading to different selective regimes:

- a) if the wasp oviposits during early gall growth and terminates growth, plants will be selected to facilitate wasp use.
- b) if the wasp oviposits after gall growth is finished (and just picks smaller galls), plants don't care what wasps do (no selection on plants except indirectly through selection on flies), and flies will be selected to increase gall size so as to avoid being parasitized.

Option b wins; the wasps have a short ovipositor that can only reach into small (& thus thin-walled) galls. A selection intensity of 0.5 favored the fly to induce larger galls. Anecdotally, this selection pressure may be opposed

by pressure caused by woodpeckers & chickadees which selectively peck open larger galls to get larvae.

**Wills, C., Condit, R., Foster, R. B., and Hubbell, S. P., 1997.** Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proc. Natl. Acad. Sci. USA* 94:1252-7.

**One sentence summary (plus a bit):** Rank-order correlation analysis shows major intraspecific density-dependent effects on recruitment and increase among trees on BCI. This and additional analysis suggest that "species herd-immunity" to specialized pests rather than intraspecific competition or abiotic density-dependence is the primary factor.

This article presents two analyses of tree species diversity in a 0.5 km<sup>2</sup> plot on Barro Colorado Island (BCI) in the Panama Canal. The trees in the plot were censused in 1982 and 1990; the relevant data are basal areas in 1982, survival from 1982 to 1990, and recruitment from 1982 to 1990, where a tree is said to recruit when it attains breast-height diameter 1 cm. Partitions of the plot into quadrats of 10, 20, 50, and 100 m on a side were analyzed. The first analysis treated the 84 commonest species in the plot. In each quadrat, the 84 species were ranked in orders including by total basal area in 1982 (A), by per-capita survival from 1982 to 1990 (S), by per-adult recruitment from 1982 to 1990 (R), and by per-capita recruitment minus mortality from 1982 to 1990 (r); A was used as an index of biomass. For each species, at each quadrat size, the correlations of the ranks of A and S, A and R, and A and r were computed, and their significance was assessed using a shuffling method, discussed below. For most species, at some quadrat size, the correlations of the ranks of A and R and A and r were significantly negative---there were major intraspecific density-dependent effects on recruitment and increase. Some of this may be due to intraspecific competition, but "[t]hese species are not producing thick ranks of seedlings that are subsequently thinned." (p. 1256) For comparison, 84 species pairs were chosen at random, and at each quadrat size, the correlations of the ranks of A of the first species and S, R, and r of the second species were computed. Relatively few were significant, and there were no significant excesses of negative over positive correlations---interspecific density-dependent effects were minor compared with intraspecific ones. A peripheral analysis established that clustering by species did not decrease appreciably from 1982 to 1990---the forest was not in the process of smoothing itself out. Another peripheral analysis established that few species exhibit significant negative correlations of the rank of r with the sum of basal area over all other species in a quadrat---gap colonization did not contribute appreciably to density dependence.

The second analysis treated all 313 species in the plot. In each quadrat, average S, R, and r were computed, along with total basal area of all trees in 1982 (B), total number of all trees in 1982 (N), and evenness in 1982 (E), a measure of species diversity. At each quadrat size, the correlations of each of average S, R, and r with each of B, N, and E were computed. Just one correlation with B was significant---abiotic density dependence, due to draw-down of nutrients or build-up of toxins, was negligible. All correlations of R and r with N were significantly negative, and most correlations of R and r with E were significantly positive---on the average, crowding was bad, and diversity was good for the trees. The authors suggest that positive correlations of recruitment and increase with diversity manifest "species herd-immunity" to specialized pests. However, they acknowledge that a question arises: "Is the apparent protection afforded by diversity simply a consequence of a number of frequency-dependent mechanisms that operate independently on different species and that have nothing to do with the activities of pests?" (p. 1256) They propose that pest-exclusion experiments might answer this question.

To assess the significance of an observed correlation in the first analysis, the authors compared it with 500 correlations obtained from hypothetical plots obtained from the actual plot by swapping the basal area, survival, and recruitment data of each of many conspecific pairs. They refer to this as "removing frequency and density effects on recruitment," and they consider it "the most important advance in the current study." (p. 1255) However, in my opinion, they neither motivate nor interpret their procedure sufficiently, and some of what they do say about it makes no sense to me. E.g., they introduce it by remarking that "[b]asal area and number of trees are positively correlated, so that correlations of the form  $f(a)$  vs.  $b/a$  would be expected to be negative even if there were no density-dependence" (p. 1253); but they earlier define density-dependence as "correlations of life history parameters with total biomass at the outset of the census" (p. 1252), hence "correlations of the form  $f(a)$  vs.  $b/a$ " constitute density

dependence, by their definition. Moreover, it is unclear to me that their procedure is necessary for their conclusions. They assert that, "using this shuffling method, we could assess significance of the actual correlations more accurately than if the difference between the actual correlations and zero were used" (p. 1254), but in the absence of rigorous arguments or detailed examples, this assertion may reasonably be challenged. Obviously, they needed a way to assess the significance of an observed correlation, but why this way? I would be much happier if they had explicitly defined a statistical model and carefully developed a hypothesis test based on it (as in Dennis and Taper, 1994).

**Wills, Condit, Foster, & Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest.**

84 most common spp. analyzed in 50 ha BCI plot. Major advance of paper is methodological: randomization method (shuffling) used to construct appropriate null model in which only the effects of freq.- and density dependence are removed while the effects of limited dispersal are retained. (Spatial relationship of individuals retained in artificial data set, but characteristics - size, and whether tree recruited or died - switched for pairs of individuals). [This methodology may be emphasized as the "major" advance to cover up these authors' previous findings of no density dependence from the same plot!]

Background:

Niche partitioning models predict positive density- and frequency-dependence within species. [? because if one individual of a species is there, it means the appropriate niche requirements are fulfilled and other individuals can establish there?] On the contrary, other models predict negative density- and frequency-dependence. Abiotic models predict negative density dependence. based on removal of nutrients from the soil, or buildup of toxic waste products. Two Biotic models predict negative density dependence.

1) "simple biotic d.d. model" - pests are host-specific negative d.d. based on attraction of pests (pathogens & parasites), e.g. Janzen (1970) and Connell (1971). Pests increase the diversity of the local environment by forcing recruitment to occur away from parent trees. [also by killing off concentrations of conspecific adults?]

2) "herd immunity model" - pests are oligophagic rather than host-specific

Other biotic models in which "niches of any type are few" - do NOT predict d.d.:

3) "community drift model" - [is this Hubbell 1997?] high diversity can be maintained through a balance of regional speciation, immigration, and local extinction if competitive exclusion takes place slowly

4) Chesson & Warner 1981, Chesson 1986 [lottery model?] temporal variation in recruitment rates may give rare species a per capita freq-d. advantage

5) metapopulation source-sink models - rescue effect

Results: support biotic d.d. models (abiotic not supported because there is no negative correlation of productivity with total biomass). Community drift model not rejected however. Density- and frequency-dependence are much more pervasive than previous studies have indicated.

1. There are strong density-dependent effects on survival, recruitment, and intrinsic rates of increase. Within a species, the three tend to be lower when basal area is higher.
2. Intraspecific effects are strong compared with interspecific effects. Pairs of species were chosen & their effects on each other evaluated - no excess of negative or positive correlations above those predicted by null model were found. In other words, little evidence for between-species interactions.
3. There is evidence for stabilization of numbers of many species because of time-lagged d.d. effects Rare species have positive  $r$ , common species have negative  $r$ .

4. Patchiness of all 84 species has not changed over the short term The substantial mortality and recruitment from 1982-1990 have not altered the overall pattern of clustering; about half the quadrats had increased c.v.'s while half had decreased.
5. Data are not explained by the ability of some species to colonize gaps
6. All the common species show d.d. effects (histogram)
7. There is safety in diversity, but not in numbers Both recruitment and  $r$  are positively correlated with quadrat diversity (evenness), but recruitment,  $r$ , and survival are all negatively correlated with total number of trees in the quadrat.

**Yodzis, P.** 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69: 508-515.

**One sentence summary:** Because of indirect effects (defined as species A affects C through a chain of intermediate species;  $A \rightarrow B_1 \rightarrow B_2 \rightarrow \dots \rightarrow B_n \rightarrow C$ ), manipulating a particular species will not result in consistent, predictable effects on the abundances of other species. As an example, simply because A eats B does not mean that adding B will increase A; effects propagating through other interacting species may swamp the direct effect and lead to decreased abundance of A. Two types of indeterminacy are discussed:

- a) directional indeterminacy: the sign (+ or -) of an interaction cannot be confidently predicted (as just described)
- b) topological indeterminacy: the locations in the web (species) that experience the largest changes in response to a perturbation cannot be confidently predicted The point is that we will have a difficult time predicting the effects of human (and non-human) disturbances on systems, even when we have a lot of experimental information.

Despite the title, Yodzis explores this phenomenon via computer simulation.

16 real webs (marshes, swamps, forests, intertidal, etc.) form the basis. For each web, he randomly constructed 100 "plausible community matrices" which capture the pairwise interactions in broad terms (trophic interactions, and interference competition among basal species). Within each of the 100 matrices, each direct interaction has the same directionality (+ or -), but the strength of the interaction is randomly chosen (but is constrained within an order of magnitude; the bounds are "guessed" at based on the field data). He then simulated the effects of "press" experiments (in which the abundance of a particular species is raised or lowered), and recorded the effect on all other species. Tabulating the differences between the 100 replicates allowed characterization of each interaction as "directionally determinate" (same direction in at least 95 of the 100 matrices) or "directionally indeterminate" (same direction in < 95 matrices). Ranking of the magnitude of abundance changes in each case allowed assessment of topological determinacy; if a particular interaction was always either high or low ranking with 95% confidence it was "topologically determinate", while the other interactions were "topologically indeterminate."

Generally, about 50% of the pairwise interactions were directionally indeterminate, and high percentages (9-93%) of them were topologically indeterminate. Species richness had no effect on directional indeterminacy (once the webs contained > 5 spp.; low-diversity webs were completely directionally determinate), but increasing species richness did decrease the fraction of pairwise interactions that were topologically indeterminate. Yodzis points out that long time scales are theoretically necessary in food web press experiments so that all the indirect effects have time to propagate through. [See, however, Menge 1997 who found empirically that published intertidal experiments were long enough to correctly characterize the dynamics.]

**Zangerl & Berenbaum** 1993. Plant chemistry, insect adaptations to plant chemistry, and host plant utilization patterns. *Ecology* 74: 47-54.

**Main point:** plant chemistry, relative to larval ability to tolerate plant chemicals, explained the distribution of an insect within its host population. This gives a mechanism for the widely accepted fact that "most phytophagous insect species always attack only a portion of their host plant population (Jermy 1984)."

Parsnip and parsnip webworms. Plants that were attacked vs. unattacked in the field were assayed for furanocoumarins; levels were > 2x in unattacked. Larvae reared in the lab on unattacked plant material experienced 40% decreases in growth rates. More work was needed to figure out this correlation though, because parsnip

webworms are able to detoxify furanocoumarins (are specialists on parsnip after all!). It's not all-or-nothing though; evidence for "metabolic overload": larvae unable to detoxify and metabolize furanocoumarins above certain levels. Thus what are "qualitative" toxins to nonspecialists behave quantitatively in specialists.\* The population-level pattern is likely determined not by female avoidance of high-furanocoumarin plants (all plants receive eggs) but by death in early larval stages before obvious damage to plant happens.

[\* in contrast to Feeny's assumption that apparent plant toxins behave qualitatively]

**Zangerl & Rutledge.** 1996. The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. *Am Nat* 147:599-608.

Optimal defense theory predictions for a particular plant part:

likelihood of attack	amt of constitutive defenses	inducibility
likely	high	low
unlikely	low	high

A test with wild parsnip (*Pastinaca sativa*). Xanthotoxin (a furanocoumarin) is the defensive compound, exists at constitutive levels, and is inducible as well. Xanthotoxin reaches a peak 24h after induction.

Results supported optimal defense theory:

plant part	likelihood of attack	# of constitutive defenses	inducibility
roots	low	low	high
leaves	high (mod. damage)	intermed	intermed
rep. parts	high (high damage)	high	none

Why not go all-inducible? First, for consistently attacked parts, you will never get the cost savings of inducible defenses because you will eventually need just as much toxin (I'm guessing that, on a per-gram basis, induced toxins are more expensive than ones produced at other times b.c. the plant can choose an optimal production schedule). Second, the delay while toxins are induced may result in unacceptable levels of damage, particularly if you have irreplaceable parts (e.g. fruits in the monocarpic parsnip).

**Zangerl, A.R. & Barenbaum, M.R.** 1993. Plant chemistry, insect adaptations to plant chemistry, and host plant utilization patterns. *Ecology* 74: 47-54.

**One sentence summary:** intraspecific differences in chemical attributes of plants may explain the distribution of insect herbivores. Plants with more furanocoumarins are eaten less. Larvae that eat plants with more furanocoumarins grow more slowly.

The study species: the herbivorous parsnip webworm on wild parsnip. The adult webworms lay eggs in plants but only some larvae develop and attack plants. Wild parsnip produces three types of furanocoumarins. This production is constitutive (not induced).

Methods: measured furanocoumarin concentration in attacked and unattacked plants in the field. Experiment: fed larvae attacked and unattacked plants and measured growth rates.

Results: unattacked plants contained more furanocoumarins. Growth rates of larvae fed tissue from attacked plants were 61% faster than those of larvae fed tissue from unattacked plants.