Stachowicz Review

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1. Mutualism & facilitation

POSITIVE INTERACTIONS [1] Ameliorate stress (physical, nutritional, predation, reproductive, dispersal).
ECOSYSTEM ENGINEER Lawton, Jones modifies environment (at temporal/spatial scales beyond the organism), while KEYSTONE SPECIES Paine (1969) have influence disproportionate to biomass. FOUNDATION SPECIES Dayton (1972) major effect due to high biomass / habitat forming characteristics.
GEOGRAPHIC MOSAIC THEORY OF COEVOLUTION Interactions vary in time in space.
Examples: Espeland & Rice (2007) Theory predicts conspecific facilitation strongest in extremely low or high stress. On serpentine soils, native (hence less stressed) plants experienced less facilitation than non-natives (stressed). Holzapfel & Mahall (1999) Shrubs facilitate annuals, annuals hurt shrubs, magnitude varies over seasons. Valiente-Banuet et al. (2006) Drought-adapted Quaternary plants facilitated continued existence of Tertiary lineages. Bruno et al. (2003) reviews importance of including facilitation in ecology as a counter-pressure to competition, predation, etc. on niche size, etc.
INTERMEDIATE DISTURBANCE HYPOTHESIS results in maximum diversity. Kimbo et al. (2006) Disturbance in oyster community decreases richness and increases evenness, so diversity index unchanged.

Environmental Gradient Effects, Stachowicz & Hay (1999) Crab eats algae that grow on soft coral, also nibble bits of coral. In shallows this service is valuable because algae is common, but deeper down algae is less of a problem and the positive interaction becomes zero/negative to the coral.

Multiple mutualists Coral have multiple zooxanthellae species, one increases growth rate, the other gets bleaching resistance. Risk of bleaching varies with temperature gradient, leading coral to vary proportions of each mutualist.

2. Trophic ecology

2.1. *Trophic Cascades*

Traditionally come in two flavors: TOP-DOWN: Predators are limiting. GREEN WORLD HYPOTHESIS Hairston et al. (1960) claims that terrestrial environments are green because herbivores are regulated by predators, letting primary production dominate. The marine world is blue because it is BOTTOM-UP: nutrient resources are limiting. Only, actually seems marine systems more likely top down (kelp forests), while terrestrial systems don't often cascade, Polis et al. (2000).

Cascade patterns, Shurin et al. (2002): Cascades predominately marine. Possible reasons include simple systems, fast prey dynamics, and more homogeneous, higher consumer:producer ratio, higher PRODUCTION (rate biomass consumed by higher trophic) per BIOMASS.

Strong (1992) Cascades require top-down, low diversity. Bottom-up systems have DONOR CONTROL where prey abundance has an affect but not predator abundance. Higher diversity systems have DIFFERENTIATED COMPENSATION, buffers changes.

2.2. *Kelp Forests: top-down*

- An example top-down system with cascade effects: Higher prey lost, killer whales left to eating sea otter prey. Fewer otters, more urchins, eat up kelp forest.
- An example of alternate-stable states: Kelp forest vs urchin barrens. Storms can destroy urchin barrens allowing kelp to recover. Can also destroy overstory kelp, allowing kelp cover to increase, Ebeling et al. (1985).
- Stability-effects: Alaska low diversity, less stable than California.
- Bottom-up effects? Temperature oscillations with El Nino cycles change productivity: colder → more nutrients, fewer storms, more kelp forests. Reverse means urchins can't live off of drift kelp, eat up forest.

2.3. *Small Islands: Bottom-up*

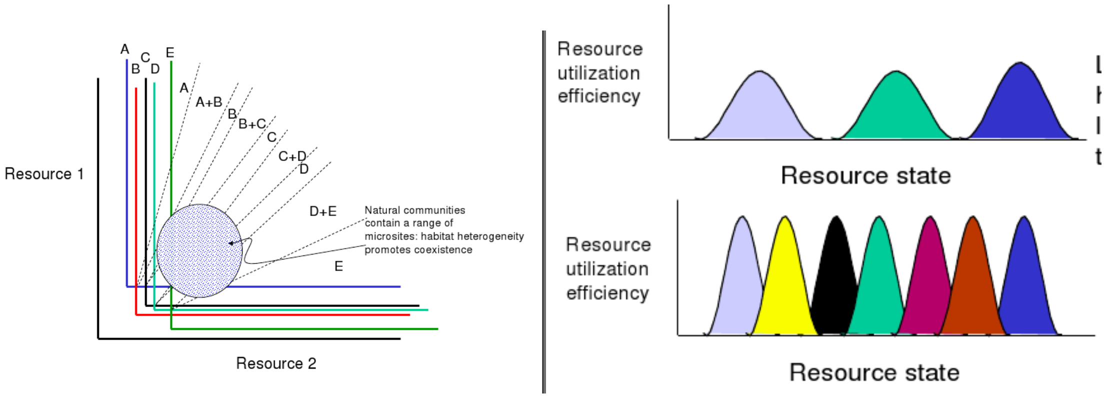
Polis et al. (1997) considers small island communities, biomass proportional to island perimeter, which determines amount of seaweed, bird guano, etc. on islands. El Nino oscillations bring rains, terrestrial plants grow, system gains new top predators (birds, parasitic wasps).

2.4. *Detecting cascades*

Frank et al. (2007) Use positive correlations between predator and prey to determine bottom-up, negative to determine top-down control. [2] Show species richness increases with being more bottom-up, but those systems also have higher temperature (and lower latitudes).

[1] Lament that more haven't read Abrams (1987) and use mechanism instead of just sign

[2] Not correct, since question is relative to who is perturbed – if fishing removes top predators, bottom-up systems should not respond.



(a) (b)

Fig. 1. Diversity, Productivity, and Stability

3. Diversity

3.1. *Definitions and Patterns*

Shannon-Wiener Diversity Index

$$\sum_{i=1}^{N} p_i \ln p_i \tag{1}$$

where frequency of the ith species in population is p_i and species richness (total number) is N. Diversity types: Alpha = within-patch, Beta between patches, Gamma is overall.

- Ecological fitting vs co-evolution. Much diversity can be explained by ecology and invasion without evolution: Janzen (1985).
- Intermediate disturbance hypothesis: High disturbance destroys most species, while too infrequent disturbance leads to competitive exclusion. Kimbro et al. (2006) show community richness decreases but evenness increases with disturbance, so no net effect on diversity. Foundation species may provide more resources or more competitive exclusion.
- Paradox of the Plankton: Hutchinson (1961) How can so many species exist on only a few resources? Temporal heterogeneity, Hutchinson (1967).
- Latitudinal gradients, e.g. Willig et al. (2003)

(i) Geographic constraints hypothesis – pencils in a box
(ii) Productivity, Energy, Area
(iii) Evolutionary speed – faster diversification rates (speciation relative to extinction), due to higher temp and solar radiation, hence shorter generations, more mutations, higher population sizes, etc. Weir & Schluter (2007) age of divergence in sister taxa in mammals and birds, shows both rates faster in poles, and diversification rate faster in poles. Try to reconcile by difference in rates higher at equator?
(iv) Weins & Donoghue (2006) More polar species almost always embedded in a tropical clade, implies tropical clades older and hence more time to diversify. Probably because glaciation etc. drives species out of poplar regions periodically, forced to recolonize more recently.
(v) Diversity (feedback and the importance of circular arguments)

3.2. *Maintenance of Diversity*

Chesson (2000) classifies all mechanisms as either: Equalizing: Reduce fitness differences, or Stabilizing: Allow return to equilibrium coexistence. *Fluctuation-Independent Mechanisms* include resource partitioning and frequency-dependent predation. *Fluctuation-Dependent* include nonlinear competition and Storage Effect: temporal (plankton) / spatial (Huffaker (1958) mites & oranges) niches.

3.3. *Function of Diversity*

3.3.1. *Diversity-Stability*

May (1973) demonstrates that randomly assembled communities are less stable when more diverse. Theoretical and experimental results have both varied. Diverse California kelp forest not as vulnerable to cascades as less rich Alaska forests.

3.3.2. *Diversity-Productivity*

- Diversity highest at intermediate productivity – low productivity diversity is limited by resource availability, high productivity limited by competition. Demonstrated in Worm (2002): adding nitrate to the low productivity site increased diversity, while adding to the high productivity site decreased diversity.
- Tilman R^* zero-isoclines – heterogeneous habitat promotes coexistence. See Fig 1(a). Packed niches utilize all resources more efficiently. More productive, harder to invade etc. See Fig 1(b). Known as Complementarity, raising productivity by avoiding overlap and hence using more resources than otherwise possible. Experimental evidence in Tilman (2001) increased biomass over 4 years in grass plots with different diversity.
- Loreau et al. (2001): A problem of scale Fig. 2. To investigate diversity $\implies$ productivity, people look at local scale, fixing conditions for a patch and varying community richness. Find productivity simply increases with diversity, as seen by the sideways figure. Productivity $\implies$ diversity people look at large scale, across landscape with varying conditions, find the peaked relationship.
- Sampling Effect: The higher productivity often simply the result of including a key species, Cardinale et al. (2006).

Fig. 4. Hypothesized relationships between (A) diversity-productivity patterns driven by environmental conditions across sites, and (B) the local effect of species diversity on productivity. (A) Comparative data often indicate a unimodal relationship between diversity and productivity driven by changes in environmental conditions. (B) Experimental variation in species richness under a specific set of environmental conditions produces a pattern of decreasing between-replicate variance and increasing mean response with increasing diversity, as indicated by the thin, curved regression lines through the scatter of response values (shaded areas).

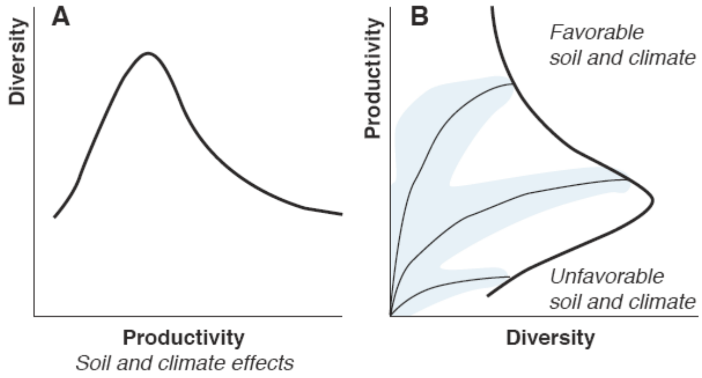


Fig. 2. Loreau et al. (2001)

4. Global climate change

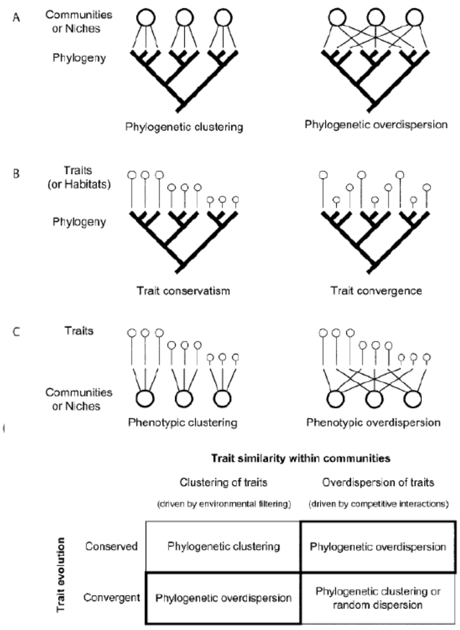
4.1. *Climate change patterns*

- Geochemistry: Greenhouse effect, CO_2 concentrations cycle with temperature. Glacial periods indicated by low sea levels, oceans enriched in heavy ^{18}O. Sea level changes between glacial periods around 150 meters.
- Astrophysics: 3 oscillations: tilt of earth's axis goes from 21.5-24.5 degrees on 40,000 yr period, eccentricity changes on 100,000 yr period, and precession are tilt and eccentricity aligned – makes earth closest to sun NH summer. Drive glaciation cycles (Moran effect).
- Oceanography: Glacial periods: cooler poles, less evaporation, lower salinity, slows the global conveyor belt currents. Hence CO_2 sequestered in deep oceans, lowers temperatures slowly. Interglacial transition is rapid, since more evaporation, raises salinity, conveyor belt currents release much sequestered CO_2.

4.2. *Types of ecological consequences*

Classification from Walther et al. (2007)

(i) Phenology: timing of seasonal activities shifts, disrupts interactions
(ii) Range shifts: Species ranges shift towards the poles. Common in glacial/interglacial, such as Lodgepole pines migration. Yet global warming may be too fast for such migration to be possible. New England marine invertebrate invaders since global warming has made winters more mild.
(iii) Community shifts: Asymmetric range shifts change community composition. Ex: Mussels on south side tidal pool vertical gradient, Harley (2003), or shift from native deciduous to invader evergreens in Switzerland, Walther (2001).
(iv) Complex dynamics Altered interactions between food webs, large scale consequences, e.g. less cold-water nutrient upwelling, recent zooplankton decline, dramatic decline in fish species richness.



5. Community Phylogenetics