# The importance of trophic status for testing community saturation patterns across multiple local and regional scales.

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## Abstract

Plots of local species richness versus regional species richness have provided a foundation for attempts at understanding the influence of regional-scale processes on local species richness. Here, we present an analysis of local species richness of rocky intertidal communities on the west coast of the U.S.A., emphasizing the importance of scale, habitat type, and taxonomic resolution. The concept of saturation of ecological communities - an upper limit to species richness imposed by local ecological interactions - theoretically should be most evident by analysis of local richness of functionally similar species across a range of regional species pool sizes. Our analysis of an enormous empirical dataset, encompassing various trophic levels and functional types, indicates that saturation is not a common feature of all intertidal communities. Nonetheless, there are certain situations where saturation is evident. For example, subdividing intertidal communities into such broad groups as 'algae' and 'invertebrates' uncovers saturation patterns unobserved when all species are lumped, especially in the high intertidal. Likewise, dividing invertebrates into broadly defined feeding-guilds leads to more wide-spread saturation patterns encompassing larger local scales. These results challenge the evidently growing consensus that saturation is not a common feature of biological communities, and caution against the application of such tests to data that are a) not grouped in ecologically relevant ways, and b) are not taken at appropriate scales for the ecological interactions of interest.

## Data

At the largest scale, we pick stretches of rocky habitat that are spaced across the U.S. West Coast to represent areas that are relatively similar in physical factors. Nested within each of these areas are three sites, and nested within each of these sites are three sets of sampled transects. Transects are placed at three specific elevations (low, middle and high intertidal) and sampled using 10 randomly placed quadrats. These quadrats are used to measure the abundance of all macroscopic plants and animals.

## Analyses

Cumulative species richness was calculated for each transect, site, and area on the West coast. These were then used as estimates of the total number of species within the regional pool of that geographical region. Likewise, counts of total numbers of species within each quadrat, transect, and site were used as estimates of the total local species richness (of identifiable species, at least). Those groups of species that were unable to be resolved due to close phenotypic similarities were retained in the dataset as 'complexes', although we continue to refer to these complexes as species counts.

Data were analyzed in three different taxonomic schemes: 'All Species', where all organisms were lumped, 'Algae/Invert', where the dataset was divided into two groups based on affiliation, and 'Trophic-level', where species were divided into suspension feeders, herbivores, omnivores, and carnivores. Three tidal heights (low, mid and high zones) were analyzed individually.

Within each permutation of taxonomic scheme, tidal height, local scale, and regional scale, non-linear regressions were calculated between regional and local species richness. These techniques were computed using a derivation of a Michaelis-Menton type equation with the inclusion of a potential non-zero intercept:

*(Local Richness) = Intercept + (Vmax*Regional Richness)/(Km + Regional Richness)*

where *Km* is a parameter that influences the shape or steepness of the curve, and *Vmax* (in combination with the intercept) determine where the asymptote lies. If the data are linear (with a slope of greater than zero), the model will fit a straight line with an asymptote of infinity.

In order to compare saturation of each permutation, we use the percentage of saturation level attained by the data as an index of relative saturation level. By dividing the local species richness maxima by the estimated asymptote, we obtain a 'percentage saturation level' for any particular set of conditions. If the relationship is linearly increasing, the data reach 0% of an infinite asymptote. If the data maximum is greater than the asymptote, it is plotted at 100% for ease of interpretation.

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## QUESTIONS:

To what extent is local species richness of intertidal communities governed by regional species pools?

At what scales does saturation (a ceiling in local species richness indicating the importance of influences other than the regional-species-pool) become apparent in intertidal communities?

How do taxonomic groupings influence these results?

## TESTS & RESULTS:

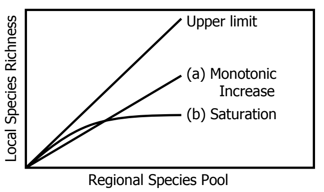


**Fig. 1:** Two theoretical relationships between regional pool of species and local species richness; (a) monotonic increase, indicating that local richness is a constant proportion of regional species pool, and (b) an asymptotic relationship indicating some point beyond which increases in regional richness no longer increase local species richness.

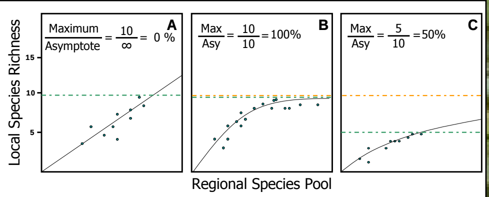


**Fig. 2:** Three examples of plausible relationships. A) The estimated line is monotically increasing, and the maximum local richness (10 species) is essentially zero percent of the estimated asymptote (infinity). B) An example of saturation, where the observed data reach the estimated asymptote of 10 species. C) A less saturated example where the data only reach 50% of the estimated asymptote. The green dot-dash line represents the highest data point, the orange dot-dash line represents the estimated asymptote.

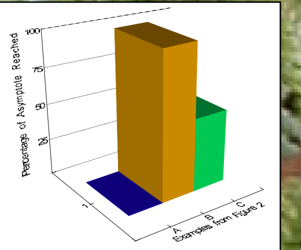


**Fig. 3:** An example of the different levels of saturation reached by figures 2a, 2b, and 2c; plotted as the percentage of the asymptote attained by the data.

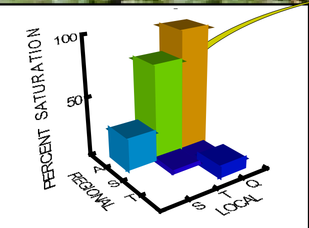


**Fig. 4a:** An example of a relative saturation plot for algae in the high intertidal. The vertical axis indicates the percentage of the asymptote reached by the data, ranging between 0% (blue bars) and 100% (orange bar). The axis on the right spans three local scales, ranging from site (S) level at left to quadrat (Q) level at right. The axis rising to the left represents various regional scales, from the area (A) level at left to transect (T) level at right.

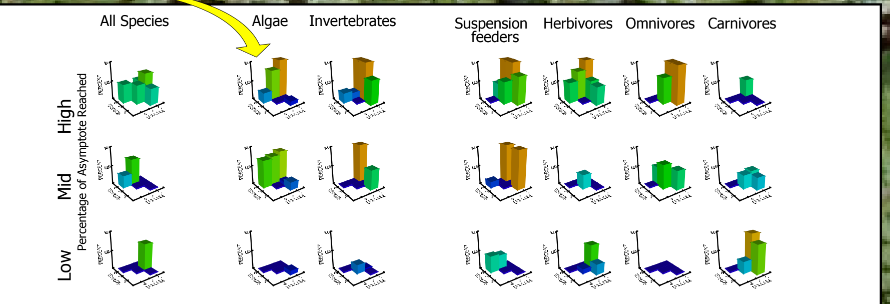


**Fig. 4b:** Relative saturation levels of various taxonomic divisions at three different tidal height levels, estimated across local and regional scales. The vertical axis indicates the percentage of the asymptote reached by the data, ranging between 0% (blue bars) and 100% (orange bars). The axis rising to the right spans three local scales, ranging from site level (at left) to quadrat level (at right). The axis rising to the left represents various regional scales, from the area level (at left) to site level (at right). Divisions across the top of the plot indicate taxonomic groupings, and the three vertical divisions demonstrate Low, Mid, and High tidal height differences.

## SUMMARY:

Both saturated and linear patterns are seen in intertidal communities.

Saturation appears more frequently (a) at small local scales in concert with large regional scales, (b) in high-zone habitats, and (c) under greater taxonomic resolution.

## WHAT DOES IT ALL MEAN?

Saturation is extremely context dependent - scale, taxonomy, and environment all alter expected results. In order for theoretical predictions to be accurate, ecological questions must be tested on appropriate scales.

Regional-level processes appear to have greatest potential to influence local species richness in low-zone habitats (low abiotic stress?).

As arbitrarily defined local scales increase in size (to 10s to 100s of meters), regional species pools appear to more strongly influence local richness; this could be due to ecologically inappropriate definitions of 'local', encompassing multiple disparate communities.

Saturation patterns are evident at small local scales (meters) in the high intertidal (high abiotic stress?), indicating that some factors other than the regional species pool (local interactions?) are strongly influencing local species richness.