

Spatial Patterns of Herbivore Impact and their Importance in Maintaining Algal Species Richness

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Coexistence of potential competitors within diverse tropical communities has often been explained as a result of fine scale resource partitioning. This is assumed to have resulted from an evolutionary history of competitive encounters and is usually inferred from shifts in abundance that occur between habitats with different physical characteristics. Seaweeds on coral reefs show predictable patterns of distribution that can be interpreted as habitat partitioning. However, manipulative experiments show that most seaweeds are habitat generalists and that both between- and within-habitat patterns of distribution are often controlled by herbivores. Spatial changes in herbivore effectiveness create a mosaic of habitats that differ in the degree to which they favor poorly defended but competitively superior seaweeds versus well defended but competitively inferior ones. If herbivory is decreased, the mosaic nature of the habitat is reduced and many well defended are excluded by competition. This pattern occurs across a large range of spatial scales and can explain between habitat differences in seaweed communities that occur hundreds of meters apart, within-habitat differences that occur only a few meters apart, and microhabitat differences that

occur on a scale of centimeters or millimeters. A portion of the microhabitat pattern is created by the seaweeds themselves. For example, consumption of palatable seaweeds is significantly reduced when they grow on unpalatable seaweeds. These associational defenses increase species richness by allowing palatable forms to invade grazed areas after unpalatable forms establish and create microsites of reduced herbivory.

Foraging by reef herbivores is constrained by a number of habitat characteristics that do not directly affect reef macrophytes. For the seaweeds, this produces a spatial mosaic of selective regimes and results in elevated species richness for the reef system as a whole.