HERBIVORES AND THE DYNAMICS OF COMMUNITIES AND ECOSYSTEMS

Nancy Huntly

Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209-8007

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INTRODUCTION

Herbivores are taxonomically and ecologically diverse, ranging in size from microscopic zooplankton to the largest of land vertebrates. Aquatic grazers include zooplankton (28, 182), larger invertebrates such as snails, insects, and crayfish, and vertebrates such as waterfowl, tadpoles, fish, muskrats, and moose (11, 27, 73, 115, 162, 163). Insects and mammals are the most conspicuous terrestrial herbivores (2, 46-49, 125), but nematodes (20), crustaceans (152), molluscs (78), birds, and reptiles (69) can also be significant. Marine ecosystems are grazed primarily by crustaceans (57, 79, 112, 143), molluscs (15, 126), fish (83, 84, 92), echinoderms (24, 25, 65), and a few insects (170), reptiles and mammals (123, 185).

These herbivores affect plant communities in many ways. Feeding selectivity and feeding modes are highly varied; the terrestrial insect herbivores alone include phloem and xylem feeders, root grazers, gall formers, and foliovores that mine, chew, roll, rasp, or pit leaves (194). Herbivores may select among plant parts, individuals, species, patches, and portions of landscapes (7, 55, 83, 95, 120, 126, 137, 138, 140). Many herbivores also clip or tear loose much plant biomass that is not consumed (5, 70, 104, 105, 122, 169). Herbivores change the environment by their trails, burrows, wallows, den building, foraging, social behavior, and other activities (1, 4, 15, 40, 50, 53, 94, 96, 98, 138, 148, 165, 167, 177). They convert plants into dung, frass,
feces, urine, and other excretions which can alter local nutrient availabilities (11, 24, 50, 52, 138, 140, 182). Additionally, herbivores may be vectors of plant disease (14, 145, 161).

The plants consumed by herbivores include single-celled and colonial phytoplankton, macroalgae, bryophytes, ferns, and angiosperms. There is a great variation in form and function within each of these groups. Marine plants include kelps, algal crusts, folioids and filamentous algae, seagrasses, phytoplankton, and periphyton (53, 54, 79, 128, 185); terrestrial angiosperms range from grasses and forbs to shrubs and trees (46); and aquatic ecosystems have plankton, periphyton, and emergent and submerged macrophytes (123). Even single-celled plants are diverse, including silica-impregnated diatoms and nitrogen-fixing blue-green algae, and they span five orders of magnitude in cell size (79, 112, 182, 190).

Given the vast variety and complexity of plants, herbivores, and their interactions, it is easy to conclude that a general understanding of how herbivores affect communities and ecosystems is not possible. Nevertheless, herbivory can be understood in a general way, and a variety of well-developed theory exists for doing so. Experiments have established that herbivores can significantly alter community structure and dynamics (e.g. 10, 24, 26, 48, 65, 73, 80, 83, 95, 97, 98, 115, 120, 126, 139, 140, 163–165), although they do not always do so (24, 48, 65, 70). Here, I attempt to put these results in context, asking (a) by what mechanisms do herbivores influence communities and ecosystems, and (b) whether the importance of herbivory to community dynamics varies systematically among ecosystems or habitats. I focus on effects of herbivores on plant diversity species composition, standing crop, and productivity, and I compare results from terrestrial, aquatic, and marine ecosystems of various types. Effects of herbivores ramify to higher trophic levels (e.g. 96, 148), but these are not considered in detail here.

The literature on plant-herbivore interactions is extensive, and I have selectively cited more recent studies. To emphasize effects shown to occur in nature, I cite primarily field studies. Much literature deals with effects of herbivores on plant individuals or single populations; often these studies don’t include information necessary to infer what patterns will be produced at higher levels of organization. Reviews that include more laboratory or behavioral and population studies are available for specific ecosystems and herbivore groups (26, 31, 46–49, 73, 85, 92, 111, 114, 115, 122, 125, 128, 174, 182).

**BY WHAT MECHANISMS DO HERBIVORES AFFECT PLANT COMMUNITIES?**

Herbivores can affect the numbers, kinds, or relative abundances of plant species in a community by several conceptually distinct mechanisms. These
mechanisms aren’t mutually exclusive: some can operate simultaneously, and one can sometimes produce another. For herbivory to change the species composition of a community, the net effects of herbivores must disproportionately affect the growth rates of populations of plants. For herbivores to alter the diversity of a community, they must create new limiting factors or reduce the effectiveness of a factor that is limiting in their absence (36). Herbivores may cause disproportionate mortality or tissue loss rates for certain plant species (41, 77, 100, 126) and may also cause the population dynamics of co-occurring species to be linked, giving the appearance that they compete for resources (88). Additionally, herbivores may produce spatial or temporal heterogeneity in the environment or in plant demographic processes. They may affect community dynamics by causing disturbances to which plant species differentially respond (30, 53, 81, 97, 168, 179, 180), by creating distinct habitats or microhabitats (33, 83, 95, 118, 119, 138, 140), or by causing variation in plant demography through time (33–35, 67, 75, 192a). Although there are numerous biologically interesting ways for these processes to arise, there remain relatively few general ways in which herbivores can influence plant communities.

The question here is not whether herbivores increase or decrease diversity in plant communities. They can do either (77, 88, 89, 126, 149); they can do this at a variety of scales (7, 83, 97, 138, 143); and the patterns produced are dynamic, with trends often changing through time (26, 28, 97, 126). For example, pocket gophers influence diversity of successional old fields by creating initially barren mounds of soil. Plant diversity on mounds is not different from plant diversity on comparably sized plots away from mounds; however, whole field diversity tends to be increased. Whether field diversity increases depends on the age of a field. In older fields, mound soils are distinct from and retain a different flora from off-mound soils. In very young fields, these differences are minor or non-existent (97). On coral reefs, the presence of territorial fishes, roving fishes, and echinoderms can lead to patches of distinct algal composition and diversity. Algae within the grazing area of a fish, urchin, mollusc; or crab may be higher or lower than in adjacent ungrazed areas, and the relative diversity of grazed areas may change with successional stage, but overall diversity typically is higher than where herbivores are absent (24, 83, 92, 126, 143).

The question also is not whether particular plant species increase or decrease with herbivory. Under some conditions, herbivory results in a community dominated by highly productive species (11, 24, 29, 139, 164, 182); in others a community of slower-growing species results (126, 159, 178, 182). The question of interest here is how herbivory influences the dynamics of communities so that patterns of species composition and/or diversity emerge, being altered from or equal to what they would have been in the absence of an herbivore or herbivores.
Herbivores can affect plant populations either in density-independent or density-dependent ways. Density-independent herbivore effects can influence populations and communities in the same way that physical environmental conditions can, and herbivory can be a way in which effects of the physical environment are realized by plants (14, 125, 132, 187). Alternatively, herbivory can be correlated with plant density and add a density-dependent component to population dynamics (14, 38, 51). The rich variety of ways in which herbivores can contribute to population growth rates, and thus to community dynamics, makes herbivory particularly interesting. Even when the direct effects of herbivores are independent of plant density, they can cause systematic changes in species composition and diversity, through fluctuations in mortality or shifts in the relative importance of different limiting factors (34–36).

Compensatory Herbivory
Compensatory effects are those that disproportionately affect populations that are common or are capable of becoming more common in a community (143). Herbivores can affect plants in compensatory ways through density-dependent or frequency-dependent damage to plants. Although it has most often been sought at the level of the foraging individual, frequency dependence can be present at the level of a foraging population without individual herbivores showing frequency-dependent preferences (32). Frequency dependence may in fact be most likely to arise at the community level, because of the combined effects of herbivores with different preferences. Ultimately, long-term coexistence is equivalent to frequency dependence (34, 35, 37), which so many mechanisms indirectly generate over the long-term.

Frequency Dependence and Density Dependence
Frequency dependence and density dependence are closely related, and frequency dependence within a community can arise from herbivores that respond in a density-dependent way to their plant resources. The critical distinction is whether the response of an herbivore is to the relative frequencies of plants of two or more species or to absolute densities of a single species. Both could occur simultaneously, and some studies show behavioral responses of herbivores to both (109, 110, 172, 173). The net effect on plants of sessile herbivores that require time to kill plants depends not only on the responses of the herbivores, but also on the response of the herbivores’ natural enemies (189). Kareiva (110) gives an example of herbivore density that is dependent on plant spacing and isolation, and in which the pattern is caused by search behavior of the coccinellid beetle predator of the herbivorous aphid.

Density-dependent herbivory can offset the tendency of a plant population to increase in abundance, monopolize resources, and exclude other species.
from a community. This is the situation described by Paine (157) in which predation by a starfish greatly reduced the abundance of a dominant consumer, allowing its competitors (which included algae) to increase. Lubchenko (126) reported a similar situation for tide pool algae and a grazing snail, *Littorina littorea*. Density-dependent behavioral or population responses of one or more herbivores can generate frequency dependence in a system of co-occurring plant populations. For instance, the antler moth, which feeds on the basal portions of grass tillers, increases in abundance as grasses increase. Ultimately, high moth densities result in sharp decreases in grass biomass, but forbs subsequently increase. As the moths are grass specialists, they fluctuate in abundance with their hosts. Moth populations are constrained also by weather, tending to reach high density only in cold springs (51). Frequency-dependent herbivory also can affect diversity. Herbivores that disproportionately damage the more common species in a patch or community tend to increase plant diversity (41, 100); those that disproportionately damage rare species (68, 158) will have the opposite effect.

Although few models have been developed specifically for herbivory, two that have invoke immediate frequency-dependent behavior of herbivores: The Janzen-Connell hypothesis of tropical forest diversity and associational resistance. The Janzen-Connell (JC: 41, 100) hypothesis describes a particular way that frequency dependence can be produced. Both Janzen and Connell hypothesized that the high diversity of tropical forests might result from disproportionate disease- or herbivore-caused mortality of seedlings growing near parent plants. Recent studies provide considerable support for the JC hypothesis. Connell et al. (43) demonstrate compensatory frequency-dependent recruitment, growth, and survival of young age classes in rain forests of tropical and subtropical Australia, but the strength of the effect is not yet clear. For three of four species of tropical trees in Costa Rican primary evergreen forest, adults were more uniformly dispersed than were juveniles, and the adults were also more uniformly distributed than would be predicted by random mortality of the extant juveniles (184). Clark & Clark (38) and Connell et al. (43) reviewed other data and found strong support for density- or distance-dependent mortality. The Janzen-Connell hypothesis has also been tested for temperate plants, including an annual grass, and found often to apply (135). At a more subtle level, Langenheim & Stubblebine (116) found that individual trees of *Hymenaea courbaril*, a tropical legume, produced seeds and seedlings of several biochemical phenotypes. Older surviving seedlings came to have only those phenotypes different from that of a nearby adult; thus, frequency-dependence occurs at the level of the biochemical phenotype.

It is clear that frequency-dependent regeneration of plants occurs. The strength of this effect, how much of it is contributed by natural enemies, and
its overall contribution to plant dynamics and diversity remain to be determined. For organisms with lifespans of centuries, frequency-dependence could arise from occasional recruitment failure, the probability of which is frequency dependent. Fluctuating herbivore populations may often cause lasting effects, the production of which can only occasionally be observed (12, 150, 198).

ASSOCIATIONAL RESISTANCE Although the Janzen-Connell hypothesis implies frequency dependence, Root (172, 173) and Atsatt & O'Dowd (6) focused attention explicitly on relationships among co-occurring plant species, suggesting that the amount of herbivory a plant experiences depends on the local species composition. Individuals of one plant species, which might most obviously be regarded as competitors, may in fact have a net positive effect on another species by deterring the amount of herbivory the other experiences; associational resistance is an indirect mutualism. Associational resistance has been proposed to result from the tendency for herbivores to be attracted to and stay in patches of high density of a favored resource, the tendency for diverse stands to harbor more natural enemies of herbivores, chemical or structural interference with herbivore location or consumption of plants, and attraction of herbivores to alternative food plants (6, 172, 173).

Associational resistance has been demonstrated for marine algae (84) as well as for terrestrial plants (6, 16, 99). It also may be a mechanism contributing to differences in plankton composition between littoral and pelagic zones of some lakes (123), and to decreased loss rates of edible algae associated with large inedible ones (175, 182). Associational resistance may arise from events occurring during a single stage of a plant's life cycle, as when one plant species provides another with protection from herbivory during seedling or sporeling establishment (6, 133, 134, 187). A tendency for one plant species to establish only under another can lead to long-term cyclical replacements (192).

The effectiveness of associational resistance can depend on the foraging selectivity of an herbivore. Buffalo and wildebeest grazed a lower proportion of Themeda triandra, a palatable African savanna grass, from plots with higher proportions of less palatable species. However, this associational resistance was not effective for zebra and Thompson's gazelles, which are smaller and more selective feeders, and which fed without respect to the relative abundances of palatable or unpalatable plants (137). The tendency for insects that are specialized feeders to be deterred by associated plants suggests that mobility or host location factors also affect the tendency for associational resistance to be effective (147, 172, 173).

Associational resistance may or may not extend to entire ecosystems (16). Some postulated mechanisms could produce lower herbivory for an entire community (e.g. enemies), whereas others (e.g. attractant plants) would
cause some species to realize increased herbivory. Proportional leaf area loss was lower in more diverse plots in successional neotropical communities. Some species experienced associational resistance and others associational susceptibility (110, 188), which may translate into apparent competition.

Clearly, associational resistance occurs in nature; its strength probably varies with herbivore and plant densities. Hay (84) demonstrated a competitive cost for palatable algae that grow in association with unpalatable algae; that cost, however, is lower than the benefit from reduced herbivory under some conditions. As a result, palatable algae are more abundant where there is at least a 20% cover of unpalatable algae when herbivorous fish are abundant. In aquatic and marine ecosystems, small herbivores such as snails or amphipods have been reported to improve the photosynthetic performance of macroalgae or macrophytes from which they graze periphytic algae (57, 123, 156). Whether periphyton or macrophytes are grazed may depend on periphyton density. More long-term and whole-system studies would greatly help to reveal the frequency of occurrence and overall significance of associational resistance.

**Apparent Competition**

Although predation, including herbivory, has often been considered to offset competition, predation can itself produce reciprocal negative interactions among prey (88–91). This relationship can arise from the joint contributions of two plant species to the population density of a shared herbivore, or from the behavior of a shared herbivore. In apparent competition, an increase in density of one plant species results in a decrease in the density of a second, not because they compete for the same resource(s), but because they are consumed by the same herbivore. Apparent competition is a sort of associational susceptibility; a plant experiences increased herbivore damage by virtue of the presence of another plant species. Apparent competition doesn’t preclude the simultaneous existence of exploitative competition for resources.

Few data exist with which to evaluate the importance of apparent competition when the linkage between plant species is strictly as contributions to an herbivore’s diet (44). However, Connell generalizes the idea of apparent competition to situations in which a shared predator is limited by the shelter provided by one plant species and then tends to eliminate other species from the vicinity of the shelter plant (9, 123, 158, 168, 175, 180). Apparent competition may contribute to habitat separation in plant communities (89, 90). Many data are compatible with this scenario, but direct tests of the contributions of apparent competition to habitat partitioning among plants have not been conducted. Apparent competition is likely to be common among plants that share herbivores, and further studies addressing this mechanism are needed.
Herbivores and Plant Competition

The effects of herbivores are realized in assemblages of plants that compete for resources or for space that allows access to resources. Herbivory is a source of loss of plant biomass or resources, and the differential effects of herbivory may alter patterns of plant performance and persistence. Traits that are positively associated with competitive ability may increase palatability to or vulnerability to herbivores. Most simply, losses to herbivores change the densities or biomasses of plant populations, but the interactions of the plants with their resources or with other plant species remain unaltered on a per capita or per biomass basis. Alternatively, herbivores may alter the density- or biomass-dependent demographic or resource depletion characteristics of plants (113). This may involve a change in plant form, phenotype, or physiology, or may involve a change in the physical or chemical environment.

Herbivory and Plant Behavior. The effects of predators on prey behavior have received much attention in systems of predators and their animal prey (111), but the potential for this idea to have value in understanding the dynamics of plant-herbivore systems has not been recognized. Although plants are almost always conceived of as having specific per capita or per biomass competitive effects on each other, these interactions are dependent on particular organismal traits and environmental conditions (81, 190, 191). Herbivory may not only decrease plant biomass but may also make a plant of a given biomass behave differently, i.e., use resources or hold space differently.

Herbivores often cause changes in plant form or physiology. Secondary chemicals (85, 108) or morphological defenses may be induced by grazing (121, 199), and growth in the absence of herbivory may differ for morphs with different defense investment (39, 83, 85, 112). For terrestrial plants, removal of leaf tissue has frequently been reported to increase photosynthetic rates of remaining leaves; however, insects that don’t remove tissue (e.g., gallers, stem borers, phloem feeders) are most often reported to decrease unit photosynthetic rates (194). Recent experiments show striking immediate carbon-flow alteration in grazed plants that presumably result in the allocation changes that emerge over longer time periods (59).

Herbivores can dramatically alter plant form. Terrestrial plants often allocate more carbon to above-ground vs below-ground tissues (23, 87, 139), or to foliage vs wood (114, 186) in response to herbivory by mammals or insects. Insect damage to terminal shoots of pinyon pines results in trees of shrubby growth form that produce only male cones (196). Similarly, removal of shoots by beavers, moose, giraffes, defoliating beetles, and a variety of other herbivores causes trees to develop a shrub, coppice, or irregular crown form (136, 139, 177, 193). Herbaceous plants also are altered in form.
and phenology by herbivory (23, 124), with grazing often producing prostrate but rapidly growing grazing lawns (80, 139, 164, 165).

Among-species differences in allocation patterns correlate with differences in competitive abilities among plants (191). Plants of similar size but different form will most likely consume resources at different rates. Herbivores frequently have distinct patterns of tissue removal or damage, and these can result in differences in function between plants affected by different herbivores. Resource use and regrowth rates differed for grasses with biomass removed in two distinct spatial patterns that simulated those produced by large grazers vs more selective insects (71). Damage to roots may result in root proliferation that decreases susceptibility to disturbance and mortality rates (176). Plants of the strikingly different forms that herbivores cause must often differ in space-holding and light-reducing characteristics, and thus they would also differ in competitive abilities. This is a plausible explanation for the higher understory biomass of herbs that occurs below browsed trees of boreal and temperate forests and of savannas. The form of a plant can also influence the likelihood of further herbivore attack, as it may influence probabilities of location by herbivores or by their predators (3). Plant form itself may limit the ability of galling insects to manipulate plant physiology and control carbon flow to their own benefit (117).

Similar herbivore-caused changes in form are reported for algae. Padina jamaicensis, a tropical reef macroalga, exists in two morphological forms, a low branched turf morph and an erect foliose form. Phenotypic transformation of individuals from the low turf to the upright foliose form results when heavy grazing by fishes is reduced, and similar morphological changes occur in two other algal species (121). Additionally, only the erect forms of these algae were observed to produce heterospores. The freshwater filamentous alga Cladophora is altered in form, from long turfs to prostrate webs, by chironomid larvae (163). In addition to changing the form or physiology of grazed plants, herbivores may cause differential representation of morphs of heteromorphic algae (127) or of physiologically differing karyophases of isomorphic algae (129).

Changes in plant form and function in response to herbivory also could occur over a longer time scale. Evolutionary changes in plant function are suggested by differences among grazing ecotypes under uniform conditions (56, 59, 139) and by biogeographic variation associated with differing grazing pressures (21, 64, 116, 153).

HERBIVORY AND THE ENVIRONMENT Herbivores may cause changes in competitive interactions among plant species because they alter the physical environment of plants. Physical factors often can be understood as changing the favorability of an environment by changing the resource uptake, growth,
or survival rates of plants (190). Thus, altering the environment can create habitats in which different sets of species persist. Differential responses of plants to the wide variety of habitat patches produced by herbivores is probably an important mechanism underlying the effects of herbivory on plant species composition and diversity.

Animals may have significant long-term effects on geomorphology (15, 45, 63, 92, 148) and geo- or hydro-chemistry (148, 159). The tree-cutting and damming activities of beaver result in long-term alteration of entire watersheds (148). Even such small animals as pocket gophers, mole rats, and ctenomyid rodents contribute to major long-term alterations of topography and soils (43). Some grazing marine fishes cause reef erosion and sedimentation by biting and breaking coral (92), and snails and fishes can alter sedimentation rates in streams, lakes, marshes, and subtidal marine habitats (15, 27, 63, 164).

Herbivores also have more immediate effects on the physical environment. Changes in abundance of freshwater macrophytes influence water flow, oxygenation, pH, and temperature of lakes and rivers (27). Gopher mounds often differ in nutrient and water contents from adjacent undisturbed areas (96). The removal of plant biomass from an area results in a decrease in the rate at which local resources are depleted, which can result in higher levels of resources for remaining or colonizing plants (96, 97, 182). Sterner (183) suggests that zooplankton change the competitive arena for phytoplankton by regenerating nitrogen and phosphorus at different rates. The responses of the algae to their resources presumably are not changed, but the resource characteristics of the environment are.

Effects of herbivory on plant behavior and on the environment intergrade. Holland & Detling (87) report evidence that the higher productivity and nutrient status of terrestrial plant communities subjected to long-term grazing result in part from alteration of nutrient cycling. They suggest that a decrease in C allocation to roots causes decreased C input to decomposers, resulting in less N immobilization and more net N mineralization. Thus, plant-available nitrogen is increased. Similarly, increases in plant allocation to secondary chemicals can affect soil microbes, decreasing plant available nitrogen (93, 159).

SECONDARY CHEMISTRY Plant secondary chemistry has been viewed as important to the dynamics of plant-herbivore systems for several decades, as secondary chemicals influence palatability of plants to herbivores (e.g. 55, 85, 122, 181). Secondary chemistry can influence plant-herbivore dynamics in two distinct ways. Levels of secondary chemicals that vary independently of the amount of herbivory a plant experiences contribute to determining environmental favorability for both plants and herbivores, and thus to setting
their population levels (14). Levels of secondary chemicals that change in response to herbivory may increase or decrease susceptibility to herbivores, adding density-dependence to the dynamics of both plant and herbivore populations (14, 60, 61, 108). The effects of secondary chemistry on plant-herbivore dynamics need not be direct but can be realized via routes involving the natural enemies of herbivores. Secondary chemicals may decrease herbivory by increasing predation on herbivores (166) or may increase herbivory by reducing predation (84a, 106).

Secondary chemistry also can affect community and ecosystem dynamics via feedback effects on nutrient cycling. Many secondary chemicals inhibit endosymbiotic microbes that degrade cellulose and also may inhibit the decomposer microbes of soil ecosystems (93, 159). Thus, herbivory can affect nutrient cycling through effects on secondary chemistry. Pastor et al (159) suggest that herbivory causes or speeds succession from more palatable tree species, such as alder or birch, to less palatable species, such as hemlock and spruce, which may persist in part because of the effects of their secondary chemistry on nutrient availability.

GRADIENTS OF HERBIVORY  Herbivory is sometimes envisioned as varying primarily in extent, being simply a loss rate of some magnitude (190). Although herbivores are almost always at least somewhat selective, many polyphagous herbivores have similar feeding preferences (M. A. Bowers, unpublished manuscript; 122, 128, 143), and selectivity may be relatively low in situations where herbivory is high (92, 95, 151).

The idea of gradients of herbivory has had utility in explaining patterns of plant response to herbivory in many systems (83, 95, 125, 143, 151; M. A. Bowers, unpublished manuscript). Several models of herbivory postulate correlations of herbivore pressure with productivity or food web structure (28, 144, 155). Phytoplankton succession is thought to result in part from changes in grazing pressure (182). Algal diversity in the Bay of Panama was well-correlated with the number of herbivore groups removed from small plots; additional variation in algal diversity was interpreted as reflecting unique effects of different kinds of herbivores (143). M. A. Bowers (unpublished manuscript) reports similar effects of mammalian herbivores in successional old-fields. Noy-Meir et al (151) interpret differences among pastures grazed by domestic herbivores as reflecting responses to a grazing intensity gradient; however, they suggest that the mechanism of the effect switches as grazing intensity increases. At low grazing pressure, disturbance results from patchy removal of plants, whereas with high grazing differential loss rates dominate, caused by higher vulnerability to grazing for taller species. Herbivore species may differ primarily in rate of herbivory (24, 143, 182). The difference in algae found within damselfish territories vs those browsed by parrotfish may
reflect differing intensities of herbivory by the two fishes. Succession in cages that excluded all grazing fishes proceeded from green to thick filamentous red algae; succession within damselfish territories, which are grazed at moderate rates, was similar but slower, perhaps stopping at an intermediate high diversity stage. Succession outside of damselfish territories, where parrotfish graze at high rates, involved a totally different group of species, primarily algal crusts (M. A. Hixon, W. N. Brostoff unpublished manuscript).

Herbivores that forage around refuges that offer them protection from their own predators often exert extreme influence over plant communities, and the resulting patterns of vegetation can be well-explained as resulting from local gradients in amount of herbivory. Refuges cause both local grazing gradients and mosaics of patches that differ in amount of grazing. Algivorous fishes in Panamanian and North America rivers concentrate in areas with lower exposure to predators, resulting in higher algal biomass along pool edges and in pools containing piscivorous fishes (162). Reef fishes also forage near refuges (83), as do smaller reef herbivores such as urchins and crabs. These animals often shelter in crevices or holes and may cause local grazing lawns or barren areas to develop (24, 25, 31, 65, 143, 187). In lakes, crayfish and some fish may forage near shelter from predators (123). The nests, dens, burrows or other refuges of small mammals typically are surrounded by prostrate or unpalatable plants; a different community develops in the absence of these animals (4, 9, 93, 195). Gradients of herbivory also may be caused by proximity to other features of the environment, such as waterholes or streams (4, 50, 58, 105).

The outcome of moderate to high grazing often is a community of low-growing or prostrate plants with high nutrient content and productivity—a grazing lawn; however, in some cases unpalatable plants of low productivity result. These alternative outcomes seem to be the result of a balance between environmental limits on primary productivity and amount of herbivory. Rapidly growing, small or low plants result from the balance of high loss rates to herbivory against high growth rates (11, 24, 25, 27, 28, 73, 80, 115, 139, 164, 165). Grazing-resistant species predominate when plants deter herbivory by unpalatability (85, 159, 175). Similar processes occur in planktonic communities, where the outcome of manipulations of herbivory often depends on the initial species composition of plankton, particularly whether large or toxic blue-green algae are present (26, 175). In low-productivity environments, in which plant growth is limited by other nutrients (not carbon), high investment in carbon-based secondary chemicals that deter herbivory is likely, whereas in productive environments, rapid growth is the more likely response (39, 154). du Toit et al (58) suggest that grazing may sometimes increase productivity and nutrient concentration of shoots of woody plants but that these tend to be replaced by other vegetation. Presumably the difference stems from the inability of plants with high structural maintenance costs and slow growth
rates to sustain high long-term losses to herbivores. The effects on community productivity of herbivores that don’t remove plant tissue are as yet not well-studied, but appear to be much more generally negative (194).

THE COMPETITION HERBIVORY TRADE-OFF  It often is assumed that compensatory herbivory arises from a trade-off such that plant traits that result in superior competitive ability for resources or space entail higher losses to herbivores. Most often, a trade-off between rapid growth or erect form and susceptibility to herbivores is identified (83, 95, 120, 126, 156, 165). However, growth rates and maximum height and/or lifespan tend to be negatively correlated for plants (190), macroalgae (83, 120), and phytoplankton (28, 79, 112). Rapid growth requires low investment in structural tissues and high concentrations of free sugars and amino acids; thus, fast-growing plants often are preferred by herbivores (83, 130, 178). Alternatively, erect form often makes plants differentially vulnerable to a variety of grazers, because they lose more mass to herbivores that graze down through a canopy (80, 83, 139, 151, 165; M. A. Bowers, unpublished manuscript). Thus, both fugitive and resource- or space-holding strategies may engender higher herbivory. This probably explains why herbivores are sometimes reported to speed and sometimes to slow, stop, or reverse succession (19, 46, 77, 78, 126, 170, 178).

Many results are consistent with the operation of a competition/herbivory trade-off. In desert ecosystems, selective consumption of large-seeded annual plants can offset the tendency for these plants to become dominant, thus increasing plant diversity (17). Marine algae that are competitively dominant often are limited by herbivores to habitats of low herbivory (83, 120), and plants that persist as fugitives often are limited in abundance by herbivores (19, 126, 178). Recent experimental work shows that insect herbivores can prevent community dominance by goldenrod during old-field succession (W. P. Carson, R. B. Root, personal communication). Burdon & Chivers (22) suggest that specialized insect herbivores contribute to the high diversity of eucalypt forests, with each tree species limited by its own herbivore. Nevertheless, a relationship between palatability to herbivores and dominance in competition clearly does not always occur. Lubchenco (126) reports habitat-specific patterns of competitive dominance and invariant herbivore preferences such that a trade-off occurs for algae grazed by the snail *Littorina littorea* in tidepools but not on emergent substrata. Noy-Meir’s (151) results suggest that there is not a simple competition/herbivory trade-off because the mechanisms by which plants are made differentially vulnerable to herbivores also vary with herbivore type or herbivore pressure.

**Heterogeneity and the Effects of Herbivory**

Communities are dynamic, showing fluctuations, successions, and cyclical changes, and they are spatially heterogeneous (79, 146, 179, 182). This high
variability both affects and is affected by herbivores. Herbivore populations and the effects of herbivores on plants vary greatly both from place to place and over time (e.g. 25, 26, 42, 50, 51, 55, 66, 83, 92, 96, 97, 101, 102, 120, 137, 139, 177, 182, 187, 197, 198). This high variation probably contributes significantly to the effects of herbivores. Environmental variability caused by herbivores can either decrease or increase diversity, but biological details suggest that increasing diversity will be common (33–36).

Most simply, heterogeneity produces structure in populations inhabiting a heterogeneous environment. Structure can reflect age or life history stage (which may simply involve distinguishing juveniles from long-lived adult or resting stages), or phenotypic differentiation of organisms in different habitats or microhabitats. When subpopulations make distinct contributions to population growth and persistence, that structure must be taken into account to understand population dynamics (34, 35, 81, 82, 118, 119). There are several ways in which herbivores can influence plant communities by causing or responding to population structure; they may cause disturbance, may cause or respond to purely spatial environmental patchiness, and may have time-variant effects on plants.

BIOLOGICAL DISTURBANCE Both herbivory and disturbance are sources of loss for plants. Conceptual models of herbivory as biological disturbance emphasize spatial patchiness in plant loss rates, whereas those of herbivory as consumption of plants emphasize selective losses among plant populations. A model of an herbivore that clears patches is basically a model of disturbance. If the herbivore has preferences, then it is a model of nonrandom disturbance. Caswell’s (30) and Hastings’s (81) models of non-equilibrium predator-mediated coexistence are not formally different from a disturbance model; predators are simply invoked to remove plants from patches. The mechanism by which community dynamics and coexistence are affected is one of succession in discrete patches, with diversity resulting from trade-offs in colonization vs competitive ability or persistence; regional diversity tends to be promoted by the presence of patches at a variety of successional stages (36). Much of the diversity of ecosystems is realized through successional sequences which herbivores may contribute to initiating.

Herbivores often have been recognized as influencing community dynamics and diversity by producing disturbance (53, 86, 96, 97, 128, 174). In marine hard-bottom ecosystems, many sorts of herbivores scrape or otherwise clear hard surfaces or disrupt soft bottom sediments (15, 53). Terrestrial ecosystems are affected by a variety of herbivore-generated disturbances, including trails, burrows, diggings, earth mounds, and wallows (40, 45, 50, 96, 138). Equivalent disturbances may have different effects depending on precise spatial location or form or on temporally varying environmental
factors (119). Intertidal algae and a grassland forb were both less successful at colonizing small disturbances because these were grazed by herbivores that apparently gained shelter from vegetation at the disturbances' edges (168, 180). Strong recruitment of an annual grass required the coincidence of unusually wet weather with the presence of gopher mounds (86).

**SPATIAL VARIATION** Plant community composition, herbivore behavior, and herbivore population density are spatially heterogeneous (1, 8, 20, 66, 79, 83, 95, 96, 137, 138, 140, 143, 162, 187). Herbivores may cause differences in plant demography among sites or patches or along gradients. Pattern in the physical environment affects many herbivores (83, 95; 99, 109, 110, 137–141, 143, 150), and herbivores may themselves impose pattern on a landscape (7, 45, 83, 92, 95, 96, 120, 138–140, 195). Below-ground herbivores typically are aggregated on many scales (1, 20, 107), as are African ungulates (138, 140), many group-living small mammals (78, 95, 195), and zooplankton (111). Herbivores' activities cause pattern in the environment and in plant growth and recruitment across spatial scales ranging from the microscopic to hundreds of km².

Sites may differ consistently over the long term in level of herbivory (8, 83, 95, 120, 125, 162). Dry and low-nutrient sites consistently have higher densities of European pine shoot moth and western pine-shoot borer (14), and the forb *Cardamine cordifolia* is consistently more damaged by herbivores in very wet or very dry sites, resulting in habitat restriction (125). Portions of reef habitats offering shelter from predators have more herbivores (93), and differential habitat use by many other herbivores is imposed by their own risks of predation (9, 62, 95, 99, 143, 162, 187). Subtle site differences such as micronutrient levels can influence levels of herbivory (98, 141).

Herbivores can alter the physical environment experienced by plants, and plant communities frequently differ between animal-generated landforms and adjacent unaffected areas (45, 148). Gophers that move low organic matter subsoil to the soil surface produce patches that remain distinct for long periods of time (97). Herbivores defecate, urinate, or produce other excretions, which can cause net nutrient transport from one habitat to another (50, 92, 123, 138, 140) or can produce small-scale local patchiness (52, 98, 182). Urine patches produced distinct plant patches in short-grass prairie, and these patches had higher productivity and supplied a disproportionately high amount of biomass and nitrogen to herbivores (52).

Structuring of the environment by herbivores may be subtle. For instance, the vegetation over and adjacent to the underground tunnels of pocket gophers is altered (165), and the influence of tunnels may extend 0.5 m each side of a tunnel (O. J. Reichman, J. Benedict, T. R. Seastrand, unpublished manuscript). Pocket gophers also alter subsurface soil structure and nutrient dis-
tribution by backfilling old tunnels (1) and by caching vegetation or concentrating urine and feces in dens (K. C. Zinnel, J. R. Tester, unpublished data). Even hoofprints can function as distinct microenvironments for germination (78). The microscale and transient nutrient patches that grazing zooplankton regenerate are believed to be very important to productivity, coexistence, and spatial patterning of planktonic algae (79, 182, 183).

TEMPORAL VARIATION The populations of virtually all herbivores fluctuate through time, often being influenced by weather or disease (8, 10, 12, 14, 41, 84, 94, 01, 102, 103, 110, 150, 159, 175, 182, 197, 198), and thus the effects of herbivory on plant growth, establishment, and mortality rates vary. Temporal demographic rates can have major influences on the coexistence of species (33–35), and this may be an important way in which herbivory works. Fluctuations in herbivory occur on diurnal, seasonal, and multiannual scales. Occasional high densities can cause extensive damage to plants, resulting in greatly decreased growth or reproductive rates or in mortality (8, 177, 187). Noy-Meir (150) documents a case of voles increasing dramatically over a large region of Israel and causing increased abundance of forbs in pasture vegetation. This impact also varied spatially, due to the existing grazing regimes of pastures. Similarly, Berdowski & Zeilinga (12) document the replacement of heath (Calluna vulgaris) by grassland following a high density of heather beetles.

Juvenile plants may be particularly sensitive to herbivory (41, 42, 47–49, 125), so herbivores can cause fluctuations in plant recruitment. Chesson (34, 35) notes the potential for the storage effect to arise and promote diversity in systems with fluctuating recruitment. The storage effect occurs when populations recruit strongly under occasional good conditions (e.g., years in which herbivores are rare and weather is good) and subsequently retain (store) the results of that successful recruitment as individuals that are relatively invulnerable to such things as herbivores and weather. For instance, mature trees of a species that is unrepresented in the understory often are reported to occur as isolated cohorts that established during periods of low herbivore pressure (42). Pastor (159) notes adult birch persisting in an area of Isle Royale heavily browsed by moose and attributes their presence to a period of low moose numbers some 50 years previous. Tegner & Dayton (187) record an instance of establishment of canopy kelps (Macrocystis) that depended on a catastrophic die-off of sea urchins. The resting stages of planktonic organisms can act similarly as stores of recruitment bursts (112).

More subtle variation in growth periodicity of plants also is documented in response to fluctuating herbivory. Periodic cicadas, which can affect all deciduous trees of the eastern United States, cause periodic growth reductions in their host trees (107), and tree ring data identify long-term growth periodic-
ity for forest species influenced by outbreaks of spruce budworm and other forest insects (67, 171, 192a). Temporal variation in growth of individuals that can store accumulated biomass or nutrients also can contribute to species coexistence, as species can specialize on transiently occurring conditions.

These arguments suggest that effects of herbivory on ecosystems are often best understood in the context of relatively long-term dynamics. Mattson & Addy (131) argued that herbivory functioned over the long-term as a cybernetic mechanism. Although their suggestion of cybernetic regulation generally has not been supported (131, 171, 186), the point that effects of herbivores are best understood as part of a long-term process remains well-taken. How long a process depends on both the period over which environmental conditions, including herbivory, vary, and the life spans of the plants. Terrestrial ecosystems may often be understood only as systems that change over at least decades and perhaps centuries, whereas marine systems may often be understandable at the level of years (spanning the time involved in successions, the life-spans of algae, and repeated disturbances) or decades (covering the period of larger-scale climatic influences such as the El Niño-Southern Oscillation). Planktonic algae operate in part on the fastest time scales, having rapid generation times and often showing marked specialization on seasonal conditions, but algae also show long-term time trends (79). Ecologically meaningful variation may be expected in all plant communities on the scale of the life span of a top predator, as numerical responses of these feed back on density and composition of lower trophic levels (26).

VARIATION IN THE IMPORTANCE OF HERBIVORY

It is of interest to know whether herbivory may be more important under some sorts of ecological or environmental conditions than under others. At the coarsest level, this resolves to a question of regulation of trophic levels: Does herbivory significantly limit the biomass of vegetation, and thus pose a strong selective force on plant populations, under some predictable set of conditions but not under others?

Hairston, Smith & Slobodkin (HSS: 76) first took the approach of analyzing ecosystems as food chains, representing trophic levels as if they were populations. They proposed that herbivores had little impact on the dominant species within nonsuccessional (equilibrium) terrestrial communities, because the dominant herbivore populations ordinarily were limited by their predators, not their food supply. Their result assumes a food chain structured so that productivity differences flow through to the top consumer level, but populations at lower trophic levels may have their abundance determined by their predators. Several alternatives to the HSS hypothesis have been developed, each of which posits increased importance of herbivores under some
conditions. These models highlight the influences of productivity and disturbance, which are recognized among plant ecologists to have strong effects on community dynamics (74, 77, 190), and of particular species composition.

Oksanen & Fretwell (OF: 155) proposed that trophic structure varies with primary productivity; more productive communities have longer food chains. Thus, the HSS hypothesis becomes a special case, a three-trophic-level (plants, herbivores, and carnivores) ecosystem. The OF model predicts that the importance of herbivory varies with primary productivity because of this change in food chain length: In very unproductive habitats, resident herbivore populations are not supported by the low phytomass, and plants are resource limited. As productivity increases, herbivore populations can be supported and the vegetation becomes limited by herbivory. Further increases in productivity allow carnivores to persist, producing the HSS scenario. Higher yet productivity might support a fourth trophic level, resulting in herbivores again limiting vegetational biomass. Data from some tundra, island, and stream ecosystems are in agreement with the predictions of OF, as are data from many lakes (153–155, 160, 163). In terrestrial ecosystems, the OF hypothesis seems supported for very unproductive and moderately unproductive environments. However, it is not yet clear whether herbivory is less limiting to vegetation significant in more productive habitats or whether primary productivity typically is the major determinant of food chain length. Although the OF model seems to have been particularly successful in predicting dynamics of aquatic ecosystems, their food chain lengths seem often to be less than productivity could support, due to such things as winter fish kills (175).

The OF model has been challenged because of its assumption that the dynamics of predator-prey interactions are laissez-faire, i.e. that the functional responses of predators are influenced only by the density of their prey, not by predator density. Arditi et al (5) propose a ratio-dependent model, which makes dynamics dependent equally on predator and prey densities. This model predicts that, at equilibrium, all trophic levels increase proportionately with productivity, and the authors view the commonly observed positive correlations of plant and herbivore biomasses, nutrient supply, and productivity as evidence that ratio-dependent dynamics are the rule. However, linear regressions probably provide little power to distinguish between two hypotheses that both predict a generally positive association of these parameters over many productivity ranges, and the nonequilibrium dynamics of the two models are similar.

Carpenter & Kitchell have emphasized dynamics within trophic levels in food chain models such as OF, and they have proposed the cascading trophic interactions hypothesis (CK: 27). CK predict that predators, including herbivores, regulate the productivity of lower trophic levels by determining species composition of their prey. Thus, potential productivity is set by the physical environment, including inherent fertility and climatic effects, but actual
primary productivity reflects also the particular species that become dominant, their growth rates, and the nutrient cycling regime. A small plankton biomass with a high productivity is predicted to result from moderately high grazing, which favors algae with high growth rates and keeps the pool of nutrients circulating more rapidly. Cascading trophic interactions have been demonstrated in many lake ecosystems (26, 28, 175), and Pastor et al. (159) apply this idea to boreal forest ecosystems. Cascading trophic interactions are one way in which herbivory can alter plant community productivity.

Ecologists working in marine ecosystems have emphasized the role of physical or physiological stresses, such as wave disturbance or desiccation associated with tidal flow (42, 144). The most recent synthesis of these ideas is that of Menge & Sutherland (MS: 144). They postulate that organisms at higher trophic levels are differentially vulnerable to stresses, with sessile organisms, including plants, being least susceptible; thus environmental stress is predicted to reduce the importance of herbivory. Menge & Farrell (142) recently reviewed results of a wide variety of experimental studies in marine ecosystems and concluded that the MS model does not apply to terrestrial, planktonic, or marine subtidal habitats, but that it may be useful in understanding marine intertidal habitats.

CONCLUSIONS

Herbivores can be understood as influencing plant communities via a few general sorts of processes. Herbivores influence growth, recruitment, and mortality rates of plants and may do so in ways correlated with plant density, frequency, or other neighborhood traits, or with competitive abilities. Herbivores may increase, offset, or generate reciprocal negative interactions (competition) among plants. Herbivory is highly variable in space and in time, and these spatial and temporal patterns of herbivory can generate structure in plant populations, the existence of which strongly influences community dynamics. Effects of herbivores are most interpretable when measured in terms of rates of plant growth, reproduction, dispersal, recruitment, and mortality for subpopulations that reflect the range of conditions plants experience. Field studies should be designed to evaluate the contributions of particular mechanisms to herbivore effects, not simply to determine whether communities differ when herbivores are present or absent.

The studies reviewed here suggest that the mechanisms by which herbivores influence plant communities do not differ fundamentally for terrestrial, aquatic, and marine ecosystems. Herbivory can significantly alter community composition and productivity in all ecosystems. Secondary chemistry is an important influence on herbivory. It may be a cost to plants and herbivores, thus setting limits to population density. Also, levels of secondary chemicals may covary with herbivory, producing density-dependent population dynam-
ics. Herbivores often are observed to be constrained in their foraging to specific areas or microhabitats; the result is strong spatial gradients and mosaics in amount of herbivory and thus in plant composition. Keystone herbivores, which cause development of a fundamentally different biological community, often with strongly altered ecosystem-level characteristics, have been demonstrated in marine (63; M. A. Hixon, W. N. Brostoff, unpublished manuscript), terrestrial (18; W. P. Carson, R. B. Root, unpublished data) and freshwater (26, 175) ecosystems. Examples also exist of herbivores that cause changes of the keystone sort in ecosystems but that do so primarily by changing the physical environment rather than by consuming plants (96, 148). Data are as yet inadequate to evaluate the relative contributions particular mechanisms make to the overall dynamics of plant communities.

There are more direct experimental demonstrations of the effects of herbivores on plants in aquatic and particularly marine ecosystems than in terrestrial. This largely reflects differences in the temporal and spatial scales at which these ecosystems vary. Marine ecologists frequently observe full successional sequences in short time periods (142). For an extreme example, a significant 25% increase in algal diversity and 36% decrease in algal productivity occurred within 5 days of the die-off of a major grazing urchin (Diadema) in a Caribbean reef ecosystem (25). Successions to and in forest, tundra, or perennial grassland may take decades or centuries. Planktonic algae have doubling times ranging from 1 day to about a week (79); this time-scale introduces its own complications; it is so rapid as to be difficult to study. These differences in time-scale of community dynamics, and thus of response to naturally occurring and experimental manipulations, reflect the different investments in structural tissues made by terrestrial plants, aquatic macrophytes and macroalgae, and planktonic algae. Terrestrial ecosystems may also be more heterogeneous than are marine systems.

Since temporal and spatial variation in herbivore populations often is high and may be of major significance, studies need to be designed to include measures of variability in herbivore impact over the range of environmental and biotic conditions that occur. We need long-term and large-scale studies, but other approaches are necessary as well. Creatively designed shorter-term and smaller-scale studies are needed, in which the environments are manipulated so the full range of conditions that occur can be observed.

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