

# Comparing aquatic and terrestrial grazing ecosystems: is the grass really greener?

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‘Grazing ecosystem’ is typically used to describe terrestrial ecosystems with high densities of mammalian herbivores such as the Serengeti in East Africa or the Greater Yellowstone Ecosystem in North America. These abundant, large herbivores determine plant community dynamics and ecosystem processes. The general concepts that define grazing ecosystems also aptly describe many aquatic ecosystems, including coral reefs, seagrass beds, and lakes, where herbivores such as parrotfishes, turtles, and zooplankton have strong impacts on ecosystem processes. Here, I compare the ecology of grazing ecosystems in search of common concepts that transcend the terrestrial-aquatic boundary. Specifically, I evaluate: 1) the feedbacks between herbivory and primary production, 2) the roles of herbivore richness and facilitation, 3) how predators and diet quality shape patterns of herbivory, and 4) how altering herbivory mediates alternative states.

## Grazing ecosystems and the role of herbivores

In terrestrial ecosystems, the term ‘grazing’ typically refers to the consumption of grasses while ‘browsing’ refers to the consumption of forbs or trees and the more general term ‘herbivory’ refers to consumption of plants in general (McNaughton and Georgiadis 1986). The term ‘grazing ecosystem’ is often used to describe terrestrial ecosystems that are dominated by large herds of migratory herbivores such as wildebeest and gazelles in the Serengeti and bison and caribou in North America (Bell 1971, Frank et al. 1998). The high biomass of herbivores in these ecosystems, typically the highest among terrestrial systems, results in herbivory being an important regulator of ecosystem processes with > 50% of primary production removed as compared to ~9% removal, on average, for other terrestrial ecosystems (Frank et al. 1998).

These characteristics also apply to many aquatic ecosystems where ‘grazing’ is often used interchangeably with ‘herbivory’ and refers to the consumption of fast-growing primary producers such as phytoplankton, filamentous algae or sea grasses. In marine systems, for example, large herbivores such as fishes, urchins, turtles and dugongs regulate primary production and community structure of coral reefs, seagrass beds and kelp forests (Burkepile and Hay 2006). Likewise, in freshwater ecosystems, waterfowl, zooplankton and benthic invertebrates impact the rates of primary production and nutrient regeneration (Lamberti and Resh 1983, Carpenter et al. 1987). Across these grazing ecosystems, 50–90% of primary production gets passed up the food chain via herbivory (Cargill and Jefferies 1984,

McNaughton 1985, Carpenter 1986). Here, I compare the ecological processes shaping grazing ecosystems across terrestrial, marine, and freshwater habitats to identify areas where cross-fertilization of ideas could be productive in facilitating the study of these herbivore-dominated systems.

There is a long history of comparing general ecological processes across wet and dry ecosystems (Strong 1992, Pace et al. 1999), and recent syntheses have identified broad patterns in plant–herbivore interactions across marine, freshwater, and terrestrial systems (Cebrian and Lartigue 2004, Hillebrand et al. 2007, Gruner et al. 2008). While these syntheses are important for understanding common patterns in ecological processes across ecosystems, limiting comparisons to systems with similar characteristics may allow a deeper investigation of the mechanisms that underlie relationships between plants and herbivores. Here, I focus on comparing the ecological processes across aquatic and terrestrial ecosystems (i.e. grazing ecosystems) that share some fundamental characteristics such as the relative high abundance of herbivores, their relatively long generation times relative to primary producers, and their relatively large body size as compared to their food source. Specifically, I evaluate: 1) the feedbacks between herbivory and primary production, 2) the roles of herbivore richness and interspecific facilitation, 3) how predators and forage quality shape patterns of herbivory, and 4) how herbivores mediate regime shifts. My goal is not to comprehensively review herbivory (Schmitz 2008) but to highlight key concepts and mechanisms where further comparative research across different wet and dry ecosystems could be fruitful.

## Herbivores and the facilitation of primary production

Although herbivory is often viewed as a negative interaction from the perspective of a plant, theoretical and empirical studies in grasslands suggest that individual plants, as well as ecosystem-level primary productivity, may respond in a neutral or even a positive manner to grazing (McNaughton 1979, Frank et al 1998). This 'grazing optimization' hypothesis suggests that plants may compensate for biomass lost to herbivory by increasing primary production following grazing (McNaughton 1979). The hypothesized mechanisms whereby herbivores facilitate plant production in these systems are that: 1) herbivores reduce self-shading in grasses, particularly by preventing the accumulation of dead plant biomass and 2) herbivores efficiently recycle limiting nutrients to back to the soil via urine and dung (McNaughton 1979, 1983). Although the hypothesis is controversial (Briske 1993), empirical work in North American and African grasslands shows that grazed grass communities can produce more biomass over the course of a growing season as compared to ungrazed areas (McNaughton 1979, 1985, Frank et al. 2002).

In pelagic aquatic systems, herbivory is unlikely to release single-celled phytoplankton from self shading, but herbivorous zooplankton are important recyclers of limiting nutrients that stimulate primary production (Sternner et al. 1992). The stoichiometry of the nutrients (nitrogen:phosphorus) recycled by zooplankton can determine the impact of primary production (Elser and Urabe 1999, Sternner and Elser 2002). The stoichiometry of zooplankton-derived nutrients may even control primary production on a global scale in pelagic marine ecosystems. A modeling study suggested that herbivorous zooplankton with high nitrogen demand recycle low N:P ratio wastes which favors phosphorus-limited,  $N_2$ -fixing phytoplankton that, in turn, facilitate nitrogen-limited phytoplankton (Nugraha et al. 2010). This stoichiometric focus is missing from many terrestrial studies of herbivore nutrient subsidies as the focus is typically on nitrogen input with little emphasis on how this impacts eventual phosphorus limitation.

For many subtidal marine systems, as in grass-dominated systems, intense herbivory keeps primary producers in short, fast-growing growth forms where there is minimal self-shading and competition for light. Seagrass beds may be the best analogs to terrestrial grazing ecosystems where dugongs, turtles, fishes and urchins can graze up to 90% of primary production (Heck and Valentine 2006). These large grazers can increase primary production by up to 40% over ungrazed areas by removing heavily-epiphytized, seagrass blades which relieves light limitation and facilitates the production of new, fast growing shoots. (Valentine et al. 1997, 2000, Moran and Bjorndal 2005). Likewise, grazing by herbivorous urchins in coral reef systems can increase algal production by 3–4 times over ungrazed areas (Carpenter 1986). Wave motion and currents would make it unlikely that herbivores could fertilize most benthic primary producers directly via their excretions. Yet, herbivores may indirectly fertilize benthic primary producers as the short primary producer canopy created by grazing

facilitates the flux of nutrients from the water column to the producers thereby decreasing nutrient limitation (Carpenter and Williams 2007). Herbivores may also facilitate primary production by altering primary producer species composition such as on corals reefs where herbivores prevent colonization of larger macroalgae which have slower growth rates than filamentous algae (Bruno et al. 2006). This mechanism is likely at work in terrestrial systems as well since removal of grazers leads to encroachment of woody vegetation (Bond 2008) that is likely less productive on an annual basis. Smaller crustaceans and gastropods across a range of benthic freshwater and marine ecosystems may also facilitate production on grazing lawns of microalgae (Lamberti and Resh 1983, Jaschinski and Sommer 2010) by preventing self-shading, facilitating nutrient flux to the algae, and/or recycling limiting nutrients given their close spatial relationships with their prey base (Bracken and Nielsen 2004).

Although herbivores can facilitate primary production across a variety of ecosystems, many studies in both terrestrial and aquatic systems document suppression by or no effect of herbivory on primary productivity rather than facilitation (Zieman et al. 1984, Williams 1988, Briske 1993, Knapp et al. 2012). Overall, facilitation appears strongly dependent upon grazing intensity and resource availability. Herbivores can facilitate primary production at low to medium grazing intensity but suppress production at higher intensities (McNaughton 1983, Hik and Jefferies 1990). Further, resource availability appears to drive much of the context-dependency in facilitation of primary production. In terrestrial systems, herbivores are most likely to facilitate primary production when water is not limiting (Augustine and McNaughton 2006) but either light or soil nutrients are limiting such that herbivores either remove plant biomass to increase light availability or recycle nutrients to the soil to remove nutrient limitation (Milchunas and Lauenroth 1993, de Mazancourt et al. 1998). Likewise in seagrass ecosystems, facilitation may be resource-dependant as urchins increased seagrass production under high light intensity (shallow areas or during summer) but not under low light intensity (deeper seagrass beds or during spring) (Valentine et al. 2000). Thus, the potential positive feedbacks between grazing and primary production are likely spatially discrete and depend on the context of abiotic factors that influence the potential rate of primary production (Fig. 1).

Work in terrestrial and pelagic aquatic systems has led the way in fleshing out these context-dependent factors, but more emphasis is needed to understand under what conditions herbivores suppress or facilitate production in benthic aquatic systems. For example, given that turbulence strongly influences nutrient limitation in benthic marine producers (Carpenter and Williams 2007), grazing may facilitate primary production in areas of moderate turbulence where grazing-induced alterations to the producer canopy maximizes nutrient delivery to the benthos while suppressing production in areas of lower flow. Thus, facilitation may be more prevalent on the edges of seagrass beds rather than the interior where the surrounding seagrass canopy retards water motion or on turbulent shallow forereefs on coral reefs rather than calmer deep forereefs and lagoonal reefs.

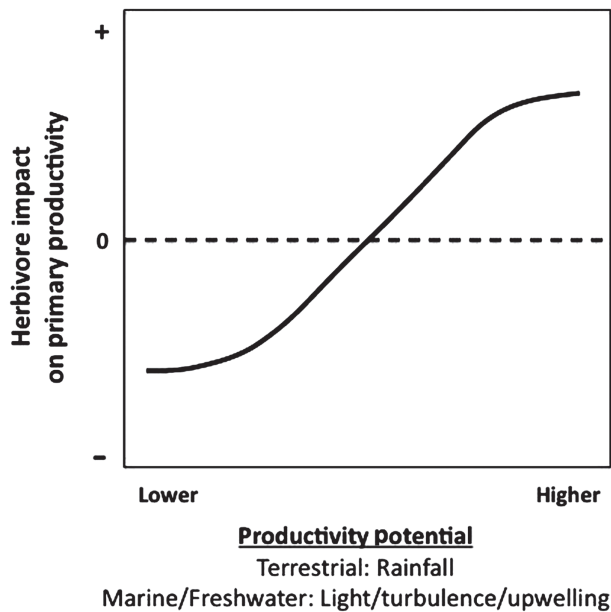


Figure 1. Conceptual graph of the relationship between productivity potential of the primary producer community and the impact of herbivores on primary production in grazing ecosystems. Herbivores will negatively impact primary production when abiotic factors controlling production such as rainfall in terrestrial ecosystems or turbulence or light in aquatic ecosystems are low. As the potential for productivity increases due to higher rainfall or increased turbulence, the impact of herbivores on primary production transitions from being net negative to net positive as herbivory maintains primary producers in short, fast-growing growth forms where they can take advantage of readily available resources.

### Herbivore richness, competition, and facilitation

The range in species diversity, body size, and adaptations to herbivory across many grazing ecosystems (e.g. 10–20 species of dominant herbivores in African savannas and 30+ on some coral reefs) sets the stage for complex interactions among herbivore species (du Toit 2003, Bellwood et al. 2004). Although low diversity herbivore guilds can strongly impact plant communities, herbivore richness appears to facilitate rates of herbivory via complementary feeding in areas of high herbivore diversity. For example, in the Serengeti, mixed-species herds of zebra, wildebeest, gazelle, and buffalo consumed 82% of plant biomass while single-species herds consumed an average of 54% (ranging from 31–74% depending on herbivore species) (McNaughton 1985). Feeding preferences for different plant species and plant heights likely facilitate efficient biomass removal. Similarly, Burkepille and Hay (2008) used *in situ* mesocosms to manipulate richness of herbivorous fishes on a coral reef in the Caribbean and showed that increasing species richness allowed for complementary feeding on different species of algae and a more efficient removal of algal biomass, which led to higher survivorship and growth of corals. Likewise, species rich assemblages of zooplankton increased grazing rates and phytoplankton removal as compared to single species assemblages (Sommer et al. 2004). Significant direct and indirect effects of consumer diversity on ecosystem function are common

across aquatic systems (Stachowicz et al. 2007), and research in these wet ecosystems has helped drive the field forward in understanding the role of consumer diversity in ecosystems given that similar experimental manipulations are intractable in many terrestrial systems.

In species rich grazing systems, the diversity of body sizes, adaptations for herbivory, and foraging scales (Cromsigt and Olff 2006), may lead to important facilitative effects among herbivore species in addition to significant effects on primary producer communities. The most common mechanism of interspecific facilitation in grazing ecosystems appears to be herbivore-mediated increases in forage quality. In terrestrial systems, large, ecosystem-engineering megaherbivores such as white rhinoceros and hippopotamus can create and maintain grazing lawns of short, nutritious grasses that facilitate nutrient acquisition by smaller herbivore species that preferentially feed in these lawns (Verweij et al. 2006, Waldram et al. 2008). Dense concentrations of smaller herbivores can also increase forage quality, likely increasing the carrying capacity of grasslands (McNaughton et al. 1997). However, these facilitative effects may only be evident during the growing season as herbivores would be more likely to compete with, rather than facilitate, one another during the dry season when plants are not growing and forage quality and quantity are limiting (Arsenault and Owen-Smith 2002, Odadi et al. 2011).

Although facilitative interactions among herbivores in aquatic systems have received much less attention, the mechanism of increased food quality via intense grazing and nutrient recycling may be similar. In both salt marshes and seagrass beds, large vertebrate grazers such as geese and turtles repeatedly graze plants, which mobilizes nitrogen from root stores and increases the nitrogen content of plant regrowth (Cargill and Jefferies 1984, Zieman et al. 1984, Moran and Bjorndal 2005, Aragonés et al. 2006). These patches of high quality forage could, in turn, facilitate nutrient acquisition in smaller herbivores such as hares in salt marshes and urchins and parrotfishes in seagrass beds. Changes to the nutrient stoichiometry of primary producers via consumer-driven nutrient cycling may also be an important mechanism of facilitation. In mesocosm experiments, Urabe et al. (2002) demonstrated that herbivorous zooplankton showed positive density-dependent growth as they recycled phosphorus back to P-limited phytoplankton, which led to increased diet quality and somatic growth of the zooplankters. Benthic freshwater grazers also show complex impacts on the stoichiometry of microalgae (Hillebrand et al. 2008) setting the table for complex facilitative or competitive effects among herbivores.

The focus on the stoichiometric relationships between herbivores and primary producers in freshwater grazing ecosystems has produced fundamental insights into the dynamic nature of the feedbacks among grazing, nutrients, and primary production (Sterner and Elser 2002). However, for some benthic marine systems and many terrestrial systems the focus is often on how grazers impact single nutrients (often nitrogen). Given that terrestrial herbivores may be more nutrient limited than their aquatic counterparts (Cebrian et al. 2009), a stoichiometric framework for understanding feedbacks between herbivores and

producers could be especially useful. Recent work showing that grasshoppers exert complex effects on plant C:N:P stoichiometry (Zhang et al. 2011) further emphasizes the need for a more explicit stoichiometric framework for understanding plant–herbivore and herbivore–herbivore interactions.

### **Top–down vs bottom–up control of grazing ecosystems**

Although the impact of herbivores on plants may be similar across these different grazing ecosystems, the relative effects of top–down and bottom–up forces on herbivore populations shows some fundamental differences between aquatic and terrestrial grazing ecosystems (Cebrian and Lartigue 2004, Shurin et al. 2006). Trophic cascades in many systems, especially aquatic ones, show that herbivores in grazing systems can be limited by predators (Shurin et al. 2002). However, the strength of the effect of predators depends on a variety of factors such as the metabolism and allometry of the herbivore and predator (Borer et al. 2005, Shurin and Seabloom 2005). The fact that trophic cascades tend to become stronger as the herbivore:primary producer size ratio increases (Shurin and Seabloom 2005) suggests that most grazing ecosystems should exhibit strong trophic cascades. However, the nutrient content of primary producers can limit the amount of herbivory in ecosystems (Cebrian and Lartigue 2004, Cebrian et al. 2009). Thus, the relatively nutrient poor primary producers in terrestrial grazing ecosystems and the subsequent nutrient imbalance in terrestrial herbivores may mean they are more often limited from the bottom–up than would be marine or freshwater herbivores (Elser et al. 2000, Hillebrand et al. 2009).

The classic grazing ecosystems of African savannas do not exhibit a trophic cascade dynamic but show strong bottom–up regulation. Predators such as wild dogs, leopard, and lion often account for 100% of mortalities in smaller herbivores such as gazelle or impala but negligible mortality for megaherbivores such as rhinoceros (Sinclair et al. 2003, Owen-Smith and Mills 2008). For medium to large-sized ungulates like buffalo and wildebeest, bottom–up processes such as rainfall and forage availability are often the main drivers of population dynamics, especially for migratory populations (Mduma et al. 1999). The quest for limiting nutrients or the highest quality forage is a strong driver of herbivore movement and habitat selection with herbivores targeting areas high in sodium, potassium, nitrogen and digestibility (McNaughton 1988, Fryxell et al. 2004). Because these herbivores are major prey for the dominant predators such as lions, these systems likely have strong bottom–up drivers that cascade through the ecosystem (Sinclair et al. 2010). The bottom–up controls on large herbivores in terrestrial systems are more evident on a global scale where rainfall and soil nutrients interact to create hotspots of high quality forage and high diversity of large herbivores (Olf et al. 2002).

Aquatic systems are much more likely than terrestrial systems to have inverse biomass pyramids with a large standing stock of predators and a high turnover of primary producer biomass (Shurin et al. 2006, Sandin et al. 2008). Recent expeditions to remote coral reefs have shown that

systems with minimal human impact have inverted trophic pyramids with top-predators such as sharks, jacks and grouper representing up to 85% of the fish biomass (Sandin et al. 2008) – the equivalent of ~5 lions per wildebeest in the Serengeti and clearly an unsustainable trophic pyramid in a terrestrial system. The longer food chains, higher predator biomass, and stronger top–down control in aquatic systems may ultimately stem from higher quality primary producers (Cebrian et al. 2009). However, herbivores in aquatic grazing systems may ultimately be nutrient limited (Hillebrand et al. 2009) which may put an upper limit on the amount of biomass that can be removed from these systems and may determine how and where these herbivores forage within ecosystems. For example, limiting nutrients, particularly nitrogen, can influence foraging decisions in herbivorous fishes, as in ungulates, as fishes target areas of higher quality forage within the landscape (Burkepile and Hay 2009).

The interaction between predators and nutrient limitation in driving herbivore foraging decisions will be a fruitful area for comparing terrestrial and aquatic grazing systems. Ungulates often select habitats to decrease predator encounter or increase the likelihood of escape once a predator is encountered (Ripple and Beschta 2004, Riginos and Grace 2008). This predator-influenced foraging can have significant impacts on the spatial impacts of herbivores on primary producers and nutrient cycling (Frank 2008). Similar patterns are well known in marine grazing ecosystems, such as seagrass beds of Western Australia. Here, herbivorous dugongs readily forage in deeper, less productive areas where they are safer from their tiger shark predators as opposed to foraging in shallower areas that have better quality forage but also a higher risk of encountering a shark (Wirsing et al. 2007). However, in the same seagrass ecosystem, green sea turtles that are in poor body condition are more likely to make foraging decisions that are riskier than those their more healthy conspecifics make in order to gain higher quality forage (Heithaus et al. 2007). Thus, foraging decisions and acceptable levels of risk are dependant on herbivore body condition and the need for quality forage. Since terrestrial herbivores are more likely to be nutrient limited and require high quality forage, terrestrial herbivores may have to make riskier foraging decisions to acquire the necessary limiting nutrients as compared to their marine counterparts. This state-dependant framework for foraging decisions should serve as a nice structure to clarify understanding of the foraging choices that herbivores make.

### **Alternative states in grazing ecosystems**

The strong interactions and positive feedbacks between plants and herbivores in grazing ecosystems suggest that disrupting these connections has severe consequences for ecosystem integrity. In fact, some of the classic examples of alternative states, or regime shifts, come from ecosystems where both primary production and herbivory are typically high (Scheffer et al. 2001). A classic example is from the strong trophic cascades in freshwater lakes where the presence of top predators, piscivorous fishes, facilitate abundant zooplankton and intense grazing on phytoplankton

(Carpenter et al. 1987). When these top predators are removed, mid-level carnivores increase, prey on zooplankton, and release phytoplankton from top-down control. The reduction in herbivory has been linked, in part, to the transition from clear-water lakes with high levels of submerged vegetation to turbid lakes with little to no submerged vegetation and abundant phytoplankton (Jeppesen et al. 1997).

Trophic cascades can also lead to an overabundance of herbivores in some grazing systems and the overgrazing of the primary producers. One classic example is the strong trophic cascade in North Pacific kelp beds where reductions in populations of predatory sea otters leads to population explosions of herbivorous urchins and the conversion of kelp forests to crustose algal barrens (Estes et al. 1998). Similarly, overfishing of invertebrate-eating fishes on coral reefs in the Indian Ocean leads to outbreaks of herbivorous urchins which overgraze the algal community and eventually feed on corals and erode the reef framework (McClanahan and Shafir 1990). Decreasing fishing pressure on predators of urchins can help reverse this trajectory. Overgrazing is common in terrestrial grazing ecosystems but is rarely linked to predator removal (Sinclair et al. 2010) and typically only happens where natural ecosystems are converted to livestock grazing with extremely high biomass of ungulates (Milchunas and Lauenroth 1993).

The integrity of grazing ecosystems also suffers when rates of herbivory decline due to overexploitation or disease. On many coral reefs, overfishing of herbivorous fishes compromises the ability of corals to recover after disturbances. When grazing is reduced, larger, less productive macroalgae often become abundant, and they can hinder coral growth, survivorship and recruitment (Hughes et al. 2007, Burkepille and Hay 2008). Thus, the removal of the herbivore from this strong herbivore-producer connection hampers the recovery of the coral-dominated state and facilitates a shift to macroalgal-dominated reefs (Mumby 2009). Similarly in terrestrial systems, the loss of large herbivores via disease or poaching leads to increased recruitment of woody vegetation (Dublin et al. 1990, Prins and Vanderjeugd 1993) which can ultimately convert open grassland to closed woodland if fire, the other major driver of woody plant abundance, is infrequent (Bond 2008).

In many of these ecosystems, the trajectory between alternative states does not follow the same trajectory forward and back along the same path, a property called hysteresis (Scheffer et al. 2001). Thus, shifting from one alternative state to another in a grazing ecosystem may take more than just reestablishing herbivore populations (or controlling overgrazing) depending on how substantial the shift in the ecosystem has become. The roles of ungulates, elephants, and fire on the transition between open savanna to closed woodland emphasizes this point. Large herbivores and frequent fires tend to facilitate a grass-dominated system and prevent encroachment of woody vegetation (Bond 2008), but removal of these herbivores can facilitate the conversion of open savannas to woodlands (Prins and Vanderjeugd 1993). Once these woodlands become established, even large herbivores such as elephants, which are uniquely destructive to large trees, seem unable to convert established woodland back to open savanna. Only an increase in fire frequency appears able to return established

woodlands to open savannas (Dublin et al. 1990). Thus, the forces that maintain savannas in open grass-dominated state (i.e. herbivory) may not be sufficient to reverse the altered woodland state. Likewise, in reef systems, the grazing pressure required to reverse a reef from being algal-dominated to being coral-dominated is much higher than the grazing pressure needed to maintain the coral-dominated state (Mumby et al. 2007). Understanding what processes control the nonlinear transitions within these ecosystems will facilitate their conservation and restoration.

## Conclusions

Recent syntheses point to key differences among wet and dry ecosystems such as higher quality forage in aquatic ecosystems (Cebrian et al. 2009) and opposite effects of nutrient loading on primary producer richness across aquatic and terrestrial ecosystems (Hillebrand et al. 2007). Yet, there are also important similarities across these systems such as similar effects of herbivores and nutrient loading on primary producer biomass (Gruner et al. 2008) and similar patterns in nutrient limitation (Elser et al. 2007). In addition to identifying broad divergence or convergence in patterns and processes of plant-herbivore interactions across ecosystems, I suggest that focusing on wet and dry ecosystems with similar inherent properties (e.g. size ratio of herbivores:primary producers, trophic structure, primary producer growth forms) may allow for a better comparison of the mechanisms that may underlie larger patterns.

A comparison of aquatic and terrestrial grazing ecosystems is useful as different ecosystems seem to be leading the way in addressing different mechanisms driving plant-animal and animal-animal interactions. For example, terrestrial ecologists have established a solid theoretical framework for examining how herbivores impact the rate of primary production across different abiotic conditions (Briske 1993, de Mazancourt et al. 1998) that could be used productively by aquatic ecologists for examining the interaction of herbivores and abiotic forcing on production. However, like Gruner et al. (2008), I suggest that research in marine and terrestrial ecosystems follow the lead of freshwater ecologists (Elser and Urabe 1999, Urabe et al. 2002) by using a more explicit stoichiometric framework for assessing how herbivores facilitate (or suppress) primary production and each other. Although recent synthesis suggests that predators control both herbivore and primary producer abundance across disparate aquatic and terrestrial ecosystems (Borer et al. 2006), in grazing ecosystems there may be fundamental differences in top-down control with stronger bottom-up forcing of vertebrate herbivore populations in terrestrial ecosystems (Mduma et al. 1999, Sinclair et al. 2010). Despite this difference, a behavioral framework integrating predation risk and resource acquisition has been useful across ecosystems for understanding herbivore foraging decisions (Wirsing et al. 2007, Schmitz 2008, Riginos and Grace 2008). The next challenge across systems ranging from savannas to coral reefs is to link these foraging decisions to spatial differences in impacts on plant communities. Ultimately, cross-fertilization of ideas among ecosystems could lead to a more unified theory of the processes and mechanisms that structure these ecosystems.

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