Green grass and high tides: grazing lawns in terrestrial and aquatic ecosystems (commentary on Burkepile 2012)

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Deron Burkepile advances a review of compelling empirical examples arguing that common mechanisms may structure grazing systems in both terrestrial and aquatic biomes. We welcome this synthesis, and on many specific points we concur. In this commentary we further develop the characteristics of grazing systems, grazing lawns in particular, reviewing their prevalence across systems wet and dry. Then, we use studies from terrestrial browsing systems – and their aquatic parallels – to explore major contrasts that are still prominent in cross-system comparisons. We rely heavily on quantitative reviews and meta-analyses to assess the prevalence and generality of the evidence for common mechanisms across grazing ecosystems. Although this approach sacrifices the detail from singular studies, it avoids undue focus on singular exceptions, instead highlighting key similarities and contrasts across biomes.

Are grazing lawns common to aquatic and terrestrial systems?

The underlying theme in the first two sections of Burkepile's review (2012) is that facilitation among herbivores and plants is a key, convergent feature common to grazing systems. This conception of grazing ecosystems traces back to McNaughton's (1984) 'grazing lawn' hypothesis for the African savannas, which lays out specific, testable predictions consistent with this intriguing theme of plant–herbivore community-wide facilitation. In the context of this Surf and Turf special feature, we ask how broadly this concept may apply across terrestrial and aquatic systems. We then highlight systems where these concepts clearly do not apply, such as terrestrial browsing systems, to explore hypotheses for the breakdown of commonalities in herbivore–plant interactions.

Setting aside the most controversial aspect – that mutual benefits to herbivore and to plant may indicate mutualistic and coevolutionary legacies (Belsky 1986) – the grazing lawn hypothesis asserts at least two fundamental, testable components: 1) moderate, and usually intermittent, grazing results in enhanced resource quality and productivity, and 2) this grazing alters producer species composition to favor communities with species traits for tolerance, rather than resistance, to herbivory (McNaughton 1984). Herbivores thus 'cultivate' (sensu Preen 1995) resources more favorable to their own persistence, growth and reproduction, and in turn herbivore pressures select for species and phenotypes that bend, but do not break, in the face of moderate consumption pressure. Burkepile does not directly address the latter component of facilitative effects of grazers, but lists two primary mechanisms for the former: the removal of senescent biomass and self-shading, and consumer-mediated nutrient recycling. These effects may also reduce plant competition for light, enhance clonal growth from underground storage tissues or meristems, and increase the photosynthetic capacity of regrowth tissues with higher nutrient concentrations (McNaughton 1984, Frank et al. 1998).

Evidence for grazing lawns is most thoroughly documented in, and appears fundamental to, the savanna biome of Africa (McNaughton 1985), but temperate grasslands in the Greater Yellowstone ecosystem (among others) offer additional empirical examples (Frank et al. 1998). In line with the central premise of this Surf and Turf paper series, studies from these two regions make up the majority of the 434 articles in Science Citation Index citing McNaughton (1984), while just 20 citations (4.6%) represent empirical or theoretical work from marine or freshwater ecosystems (as of 5 June 2012).

On land, grazing lawn systems are typified by large-bodied, homeothermic herbivores (often ungulates) consuming small-stature herbaceous plants (e.g. grasses), which are adapted to fire, drought and herbivore pressure for tolerance and rapid compensatory regrowth via stolons, rhizomes, or from basal meristems (Frank et al. 1998, Díaz et al. 2007, Skarpe and Hester 2008). Large herbivores have lower mass-specific metabolic rates and can maintain biomass on lower resources levels than smaller-bodied animals; in turn, smaller plants have higher mass-specific growth rates that can support higher consumption

rates than larger plants with slower turnover and longer generation times (Shurin and Seabloom 2005, Shurin et al. 2006). Moreover, herbivores much larger than their resource base tend to be less selective than smaller animals; plant neighbors that allocate to defensive chemistry and morphologies, in lieu of traits for tolerance and compensatory growth, may be consumed with their palatable neighbors ('associational palatability', Olff et al. 1999) without commensurate regrowth capacity. It is worth noting that these effects are likely to be spatially and temporally heterogeneous; therefore, 'lawn patches' may co-occur with less palatable patches in a landscape mosaic at local scales (Olff et al. 1999, Riginos and Grace 2008).

All of these characteristics together, however, may be insufficient to successfully predict facilitative grazing relationships and grazing lawns. Data demonstrating increased net primary productivity (NPP) with grazing are not general for terrestrial systems dominated by livestock, which generally show depressed NPP with grazing in a variety of environmental contexts (Milchunas and Lauenroth 1993). Moreover, grazers often alter plant community composition, but with varying outcomes and effects on richness and evenness, depending on baseline abiotic conditions and fertility (Olff and Ritchie 1998, Hillebrand et al. 2007). A worldwide meta-analysis of plant traits tentatively concluded that palatability generally decreased with grazing, but the authors cautioned that multiple palatability traits were pooled to achieve a statistical sample size (Díaz et al. 2007).

Although there are distinct taxonomic and physiological differences in herbivores and producers from submerged environments, numerous candidate aquatic systems mirror the criteria for grazing lawns developed from savannas. Certainly, strong empirical examples abound for grazer facilitation of NPP from phytoplankton in lakes (Porter 1976, Sterner et al. 1992) and in seagrass beds (Preen 1995, Valentine et al. 1997). As Burkepile (2012) notes, seagrass habitats appear to represent properties most analogous to terrestrial savannas. Although seagrasses are not phylogenetically related to true grasses, they share similar traits and a physiognomy consistent with adaptations to grazers (Heck and Valentine 2006, Valentine and Duffy 2006). Large-bodied vertebrate herbivores such as fishes, sirenians (dugong and manatees), sea turtles, and waterfowl can be effective grazers of seagrasses analogous to artiodactyls in grasslands (Valentine and Duffy 2006). Experiments to simulate cropping (turtles) and uprooting (sirenians) herbivory demonstrated divergent results on seagrass communities; while cropping led to increased nutrient content of regrowth tissues, uprooting changed community composition to favor more tolerant, palatable taxa (Aragones et al. 2006). Hence, the full species assemblages of historical grazers may have acted complementarily to facilitate grazing lawns in seagrass beds (Valentine and Duffy 2006), as reviewed by Burkepile for contemporary savanna ecosystems.

Aquatic periphyton – a broad grouping that encompasses the algae, bacteria and eukaryotic micro-organisms carpeting most substrates in the shallow benthos of marine coastal zones and freshwater streams and lakes – appear to offer another aquatic example of grazing lawns. However,

a comprehensive meta-analysis of grazing effects in periphyton (Hillebrand 2009) demonstrated that herbivore facilitation of productivity is not a general result. Although Hillebrand's (2009) review includes cases where grazers facilitated positive feedbacks on periphyton productivity (Lamberti et al. 1989), it documented net losses of 56% of periphyton biomass across hundreds of field experiments. Many of these experiments measured standing biomass but not NPP over time; hence they represent incomplete tests of grazing lawn predictions. However, unlike in savanna or seagrass systems, periphyton typically are small, often unicellular organisms conspicuously lacking roots, meristems, or clonal rhizomatous tissues buried in substrate refugia from grazers. Grazing arthropods, molluscs and fish rasp surfaces and unselectively remove large patches of individual organisms in their entirety, which may recolonize substrates but cannot regrow (Hillebrand 2009). Different studies have variously demonstrated both increases and decreases in the spatial heterogeneity of periphyton (Hillebrand 2008). For example, open patches may be colonized by N-fixing cyanobacteria, with the potential to increase NPP of the greater patch (Wilkinson et al. 1984, Williams and Carpenter 1997). Alternatively, unpalatable fleshy algae may take root and proliferate in place of periphyton cover (Scott and Russ 1987, McClanahan et al. 2002). Systematic reviews and conclusions about the resulting palatability of these grazer communities in marine and freshwater systems appear to be lacking.

How do grazing lawns contrast with browsing systems?

On land, 'browsing lawns' analogous to the McNaughton (1984) criteria appear to be highly uncommon, although intriguing exceptions may exist (Kuijper et al. 2009, reviewed by Cromsigt and Kuijper 2011). Browsing systems are dominated by standing biomass of taller stature, usually woody, vegetation with individual plants larger to much larger than vertebrate browsers or invertebrate plant parasites (e.g. phytophagous insects). The case from Isle Royale (Michigan, USA) exemplifies the trend that large mammalian browsers, such as moose, preferentially forage on high quality, deciduous flowering plants and shrubs (McInnes et al. 1992). This either induces resistance traits in browsed plants, or reduces their abundance relative to lower quality, more resistant trees, increases C:N ratios and phenolic compounds in foliage, and reduces mineralization rates of soil nitrogen (Pastor et al. 1993). Phytophagous insects are probably the most important defoliator of woody plants, particularly in forested systems (Haukioja and Koricheva 2000), and quantitative reviews indicate that these plant parasites routinely induce a diversity of chemical and morphological defenses in response to their feeding (Nykänen and Koricheva 2004, Kaplan et al. 2008).

A clear difference in terrestrial grazing versus browsing systems relates to the physical structure and chemistry of primary producers, which have implications for tolerance or resistance to herbivores and in the nutritive elemental content available to support herbivore populations and higher

trophic structure (Shurin et al. 2006). These fundamental contrasts recapitulate in comparisons of producers in aquatic and terrestrial biomes. Aquatic macrophytes and seaweeds in general are composed almost entirely of photosynthetic tissues, largely lack roots and vascular systems, completely lack (lignin) or contain a small fraction of the recalcitrant structural carbon (cellulose) of terrestrial plants, obtain nutrients at least in part from the water column, and rely on buoyancy rather than rigid structural tissue to orient towards light (Demment and Van Soest 1985, Hay and Steinberg 1992, Choat and Clements 1998, Elser et al. 2000). With respect to their nutritional value to herbivores, terrestrial plants have lower nitrogen and phosphorus contents and higher C:N ratios than most aquatic plants and algae (Hay 1992, Elser et al. 2000, Cebrian and Lartigue 2004, Cebrian et al. 2009). Notwithstanding these differences, terrestrial plants and many seaweeds are qualitatively similar in their use of a wide diversity of refractory secondary compounds that can deter vertebrate and invertebrate herbivory and retard decomposition (Hay and Steinberg 1992).

These contrasts in plant quality appear, in turn, to be manifest in fundamentally different trophic structures between marine and terrestrial systems. Because of the higher nutrient content and reduced structural compounds, a far greater proportion of annual net primary productivity (ANPP) is consumed, processed and remineralized in many aquatic systems, resulting in a smaller fraction of ANPP in standing producer biomass (Cyr and Pace 1993, Cebrian and Lartigue 2004, Shurin et al. 2006). Overall, the herbivore:plant (or algivore:alga) coupling appears to be stronger in many aquatic systems relative to terrestrial counterparts (Elser et al. 2000, Shurin et al. 2006, Gruner et al. 2008), and this in turn may determine the strength of higher order interactions such as trophic cascades (Shurin et al. 2002, Borer et al. 2005). As Burkepile notes, recent studies from relatively undisturbed reef systems report dramatic inverted trophic pyramids, with up to 85% of the total fish community biomass invested in top predators (Friedlander et al. 2007, Sandin et al. 2008). In savannas and grassland grazing systems, herbivores play important roles in structuring communities (Pringle et al. 2007), and top predators can be highly influential in regulating herbivores (Sinclair et al. 2003, Ripple et al. 2010). However, relative biomass of terrestrial predators is but a small fraction of grazers, and herbivore biomass is in turn but a small fraction of primary producers (McNaughton et al. 1989). Some of these differences in biomass distribution may also be attributable to the allometry of interactions; the dominant herbivores on reefs (teleost fishes) are small in body size relative to their predators, whereas many savanna grazers escape predation risk by outgrowing the dominant predators (Choat and Clements 1998). McNaughton (1984) argued for an additional 'benefit' of lawn maintenance for grazers, particularly midsize herding animals: open, cropped grassland systems facilitate greater vigilance to predators than do woodlands, which instead may hide menace behind any tree (McNaughton 1984, Riginos and Grace 2008, Cromsigt and Kuijper 2011, Burkepile 2012). Might we expect a greater prevalence of grazing lawn dynamics by focusing on schooling or aggregative aquatic grazers?

Conclusions

Burkepile (2012) offers a thoughtful comparison between terrestrial and aquatic ecosystems, arguing for key similarities in the mechanisms of consumer–producer interactions and emergent ecosystem properties. We amplify the grazing lawn concept in particular as an intriguing set of hypotheses deserving more explicit attention in marine and freshwater systems. Further, we highlight important contrasts between wet and dry grazing (and browsing) systems, the most notable of which are the qualitative differences in chemical and structural compounds in primary producers, opposing biomass distributions among trophic levels, and the corresponding disparities in intensity of top–down control. We hope these parallels and contrasts help to stimulate conversations and collaboration among ecologists working across ecosystem boundaries.

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