



Measuring ecosystem function: consequences arising from variation in biomass-productivity relationships

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Abstract: Species diversity loss is expected to alter ecosystem function, but previous work has demonstrated inconsistent relationships between these two factors. Productivity is the most common measure of ecosystem function, but given the difficulty in measuring productivity, standing biomass or change in biomass are frequently used as proxy measures. A review of the recent ecosystem-function literature revealed that 93% of studies measure productivity as biomass, thereby assuming a strong positive relationship between these two variables. We tested this assumption by measuring biomass and productivity in seagrass beds in the Gulf of Mexico. We found that the relationship between standing biomass and productivity could be positive or negative, depending on site. Change in biomass over months inconsistently underestimated short-term productivity. The relationship between biomass and productivity may depend on plant age, successional stage, or site-specific rates of tissue loss to herbivory, senescence, or disturbance. Our results suggest that if biomass continues to be used as a measure of productivity without justification, highly productive communities that typically show little change in biomass, such as healthy climax communities, will not be interpreted as such. The conflicting results of previous studies investigating the relationship between diversity and productivity may be due to differences in the inherently variable relationship between biomass and productivity at different sites and scales.

Introduction

One of the goals of community and ecosystem ecology is to assess how community-level attributes (e.g., diversity) affect how well systems function, where “function” is typically described as some measure of energy or nutrient flux. Productivity is one important measure of ecosystem function, with definitions ranging from the efficiency of energy conversion (Odum 1959) to the rate of carbon production and transfer (Gurevitch et al. 2002, Roxburgh et al. 2005). Recently, many ecologists have settled on an operational definition of net productivity as biomass produced per unit time (e.g., Ricklefs and Miller 2000, Krebs 2001, Begon et al. 2006).

Given the difficulty of measuring productivity continuously over time, many studies have relied on a variety of measures to estimate productivity. Such estimates range from annual rainfall to oxygen production measurements (Rosenzweig and Abramsky 1993) and each method comes with its own set of assumptions and limitations. Standing biomass is a commonly used proxy measure of productivity, but only provides a static measure of a dynamic variable. Change in biomass, or growth rate, provides a more accurate measure of productivity, but both standing biomass and growth rate will underestimate productivity if any tissue is lost from the primary producer.

The usefulness of biomass as a reliable predictor of productivity depends on consistent rates of both tissue produc-

tion and loss. Producers may lose tissue to a number of sources, including herbivory, disturbance, and senescence (Gurevitch et al. 2002). Effects of each of these factors often vary between sites and among systems (Menge 1976, Cubitt 1984, Cyr and Pace 1993, Blanchette 1996). Primary production may vary with season (Dayton et al. 1999), the age or size of the plant (Gower et al. 1996), or the age or successional stage of the community (Gurevitch et al. 2002). Additionally, those factors that reduce biomass (e.g., herbivory) may have positive (Paige and Whitham 1987, Valentine et al. 1997) or negative (Belsky et al. 1993) effects on productivity. This temporal variability in both biomass and productivity suggest that growth rates measured over longer time periods are more likely to underestimate primary productivity to varying degrees, potentially resulting in Type I or Type II statistical errors when considering the effect of a given factor, such as diversity, on productivity (Sokal and Rohlf 1995). Using biomass as an estimate of productivity does not require an exact 1:1 relationship between the two variables, but rather assumes a positive relationship and tight correlation between biomass and productivity over time. However, we believe that the nature and strength of these correlations are likely to be context-dependent.

In recent years, productivity is most commonly measured in studies investigating the relationship between diversity and ecosystem function. Hooper et al. (2005) recently reviewed this body of literature, and while the review was not intended to be a complete review of all productivity studies,

it did provide a reasonable sample of recent studies that measure productivity and that are likely to guide further study in this field. We reviewed those papers cited by Hooper et al. (2005) that provided empirical estimates of productivity. Of the 43 studies, 40 (93%) use standing biomass or change in biomass as an estimate of productivity. Only one of these studies justified the use of biomass as a proxy measure (Downing and Leibold 2002), while the others assumed a tight, positive correlation between biomass and productivity in their particular system. The studies span a broad range of systems, including terrestrial grasslands, tropical forests, freshwater lakes, algal microcosms, kelp forests, and seagrass beds.

Seagrass beds are among the most productive ecosystems. Seagrasses and their associated species account for much of the productivity in shallow coastal waters and provide important nursery habitat for fish and invertebrate species (Williams and Heck 2001). Seagrass beds provide an excellent system in which to measure both biomass and productivity at several scales, from individual leaves to entire ecosystems. Many studies have measured productivity and biomass in seagrass beds and have demonstrated that both vary temporally and spatially (Duarte and Chiscano 1999, Agawin et al. 2001, Fourqurean et al. 2001). Biomass and productivity are typically reported at very large scales (e.g., bays or estuaries) and on a per area (e.g. areal productivity) or a mass-specific (e.g., specific productivity) basis. Generally, there is a positive correlation between biomass and areal productivity at the large scale of bays or estuaries (Fig. 1a), but at the same scale, there is no significant correlation between biomass and specific productivity (Fig. 1b). This latter result could be indicative of different biomass-productivity relationships at different spatial scales. Biomass and productivity measured at small scales ($< 1 \text{ m}^2$), but scaled up and averaged across large regions ($> 100 \text{ m}^2$) (Duarte and Chiscano 1999, Agawin et al. 2001, Fourqurean et al. 2001), may obscure small-scale differences in the biomass-productivity relationship. Many studies in the field or in experimental mesocosms, in both marine and terrestrial ecosystems, measure change in biomass at the scale of meters or less, or at the plant level, rather than kilometers (Duffy et al. 2001, Bruno et al. 2005, Hooper et al. 2005, Bruno et al. 2006). Here we examine the relationship between biomass and productivity at this smaller scale to determine whether biomass or growth rate serve as reasonable proxy measures of productivity, especially with regard to biodiversity-ecosystem function studies (Hooper et al. 2005).

Methods

Biomass and productivity of seagrass [*Thalassia testudinum* (Banks ex König)] were measured within St. Joseph's Bay, Florida, a shallow, well-protected bay consisting of distinct patches of seagrass. We surveyed six seagrass beds in each month between June and September 2005, although not all beds were sampled in all months. Beds were separated between approximately 5 and 250 meters. The sizes of the sea-

grass beds were on the order of tens to hundreds of square meters and were quite small relative to many studies (e.g., Fourqurean et al. 2001). In August, we counted urchin densities by haphazardly throwing 12 $1 \text{ m} \times 1 \text{ m}$ quadrats in each bed and taking the average of the 12 quadrats as the estimate of urchin abundance in the bed.

The ecology and growth form of *T. testudinum* are similar to most grasses and provide an opportunity to measure growth in the absence of tissue loss. Partial tissue loss of *T. testudinum*, due to herbivory, disturbance, or senescence, typically occurs at the terminal end of the blade (pers. obs.), but growth takes place at the basal end (Zieman 1974, Valentine et al. 1997). We measured short-term growth at the basal end of seagrass blades, before the initial point of measurement reached the area where tissue loss occurs, as an estimate of productivity.

Seagrass beds are made up of few genets with underground rhizomes from which aboveground leaves grow (Tomlinson and Vargo 1966). Short shoots consist of blades clumped in groups of two to six leaves. We used short shoots in each bed as statistical replicates and measured growth and biomass of short shoots. Within each bed in each sampling period, between six and fifteen short shoots were marked with flags, initial lengths of all leaves were measured, and a dissecting needle was used to poke a small hole at the base of each leaf. These leaves were then left to grow for a sampling period of seven to fourteen days. At the end of the sampling period, the distance between the base of the plant and the hole-scar was used as an estimate of leaf growth and stand-

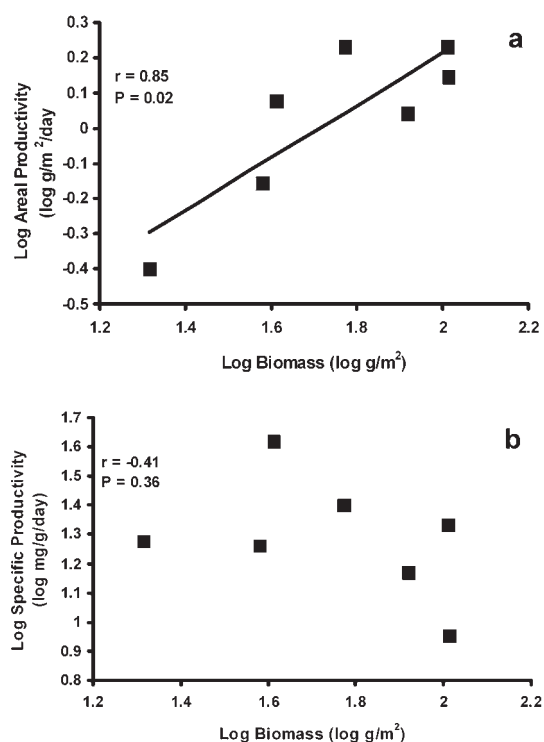


Figure 1. The log-log relationship between biomass and areal productivity (a) and leaf specific productivity (b) at seven sites in the Gulf of Mexico. Data from Fourqurean et al (2001, Table 3).

ardized by the length of the sampling period (Valentine et al. 1997). Growth was averaged among blades within a short shoot.

The average leaf length on those short shoots for which growth was measured was used as a proxy for plant biomass. To generate a leaf length-biomass regression line, we collected 20-30 leaves from each bed at the beginning of each sampling period, except in August, when leaves were collected at the beginning and end of the sampling period. The length of each leaf was recorded and then all leaves were dried for at least 48 hours in an oven at 60°C. The dry mass of each leaf (including epibionts) was recorded and leaves were then soaked in 50% phosphoric acid to remove epibionts and then dried again for at least 48 hours before measuring dry mass (Zieman 1974). The equation of the line regressing epibiont-free dry weight against length was used to predict biomass from lengths of blades from experimental plants measured in the field. Epibiont weight was determined by subtracting the final dry leaf mass from the dry mass of leaves with epibionts.

Biomass and growth data were logtransformed to meet the assumptions of parametric tests (Quinn and Keough 2002). Analysis of variance was used to compare growth and biomass among beds. Separate correlation analyses were per-

formed for each bed, using short shoot biomass and average short shoot growth as variables. All statistical analyses were performed using JMP version 4.0.4 (SAS Institute, Inc. 2001). We also compared productivity measured over two different time scales: (a) the long-term (3 month) change in biomass, measured as the difference in plant biomass between June and September, standardized by the number of days between dates and (b) growth measured over multiple seven to fourteen day periods, with little opportunity for tissue loss, standardized by the number of days of growth.

Results

Length proved to be a robust predictor of biomass; all regression lines were highly significant ($p < 0.001$) and explained at least 90% of the variance in biomass. Overall, biomass and growth estimates among beds were not significantly different [biomass ($F = 0.95$, $df = 5,416$, $P = 0.45$), growth ($F = 0.62$, $df = 5,113$, $P = 0.69$)]. However, the relationship between biomass and growth varied among beds. At the scale of short shoots, the relationship between biomass and growth was always significant, but varied from positive to negative depending on bed (Fig. 2). Out of six beds, four showed a positive relationship between biomass and growth, while two beds showed a negative correlation between

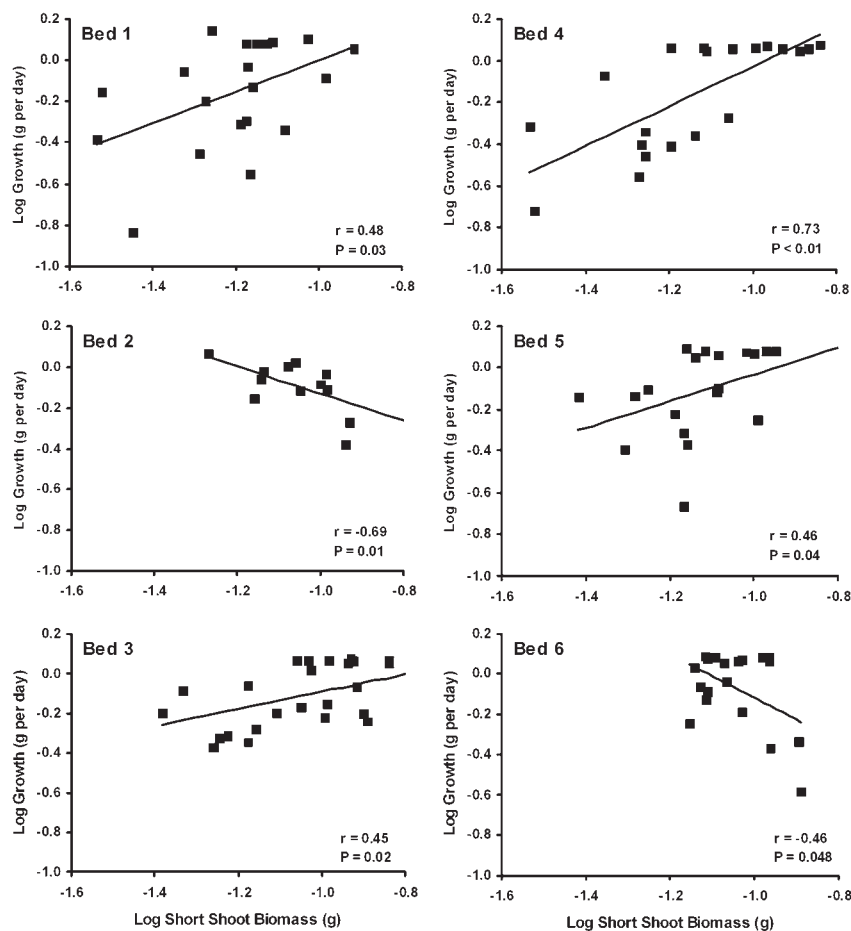


Figure 2. Correlations between short shoot biomass and growth within six seagrass beds.

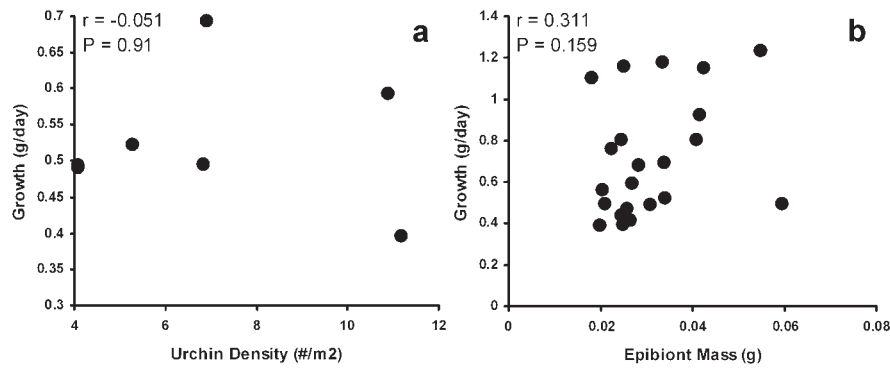


Figure 3. Correlation between growth estimates and urchin density (a) and epibiont mass (b). Neither correlation is significant.

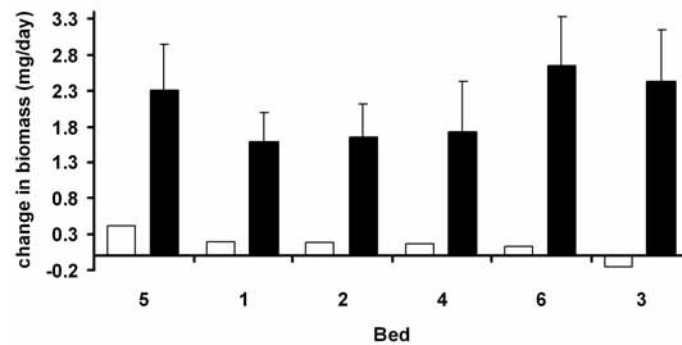


Figure 4. Productivity estimated by two different methods. White bars represent the long-term change in biomass, measured as the difference in plant biomass between June and September, standardized by the number of days between dates. Black bars represent back-transformed means and 95% confidence intervals of growth measured over multiple seven to fourteen day periods, with little opportunity for tissue loss, standardized by the number of days of growth.

biomass and growth (Fig. 2). In four beds, although the correlation was significant, the strength of the relationship was low ($r = 0.45$ - 0.48 , Fig. 2), indicating a relatively loose relationship between these two variables.

We attempted to explain the variation in productivity among beds by correlating growth in each bed with either urchin density or epibiont weight. Urchin abundance does not correlate significantly with growth estimates (Fig. 3, $P = 0.913$). Epibiont mass is also uncorrelated with growth (Fig. 3, $P = 0.159$).

Long-term estimates of productivity, measured via change in biomass over a three month period, differed greatly from productivity estimates measured by change in biomass over one to two weeks (Fig. 4). Long-term estimates of productivity are approximately an order of magnitude less than short-term estimates. In one case, the long-term measure of biomass resulted in a negative value of "productivity". Further, the rank-order of beds changes depending on which estimate of productivity is used (Fig. 4).

Discussion

The biomass or growth rate of primary producers, such as *T. testudinum*, is frequently used as a measure of productivity, but this approach assumes that there is a positive rela-

tionship between biomass and productivity and that these two variables are tightly correlated. While previous studies, particularly in marine systems, report positive relationships between biomass and productivity at very large scales (i.e., hundreds of kilometers), these measurements are typically made at much smaller scales and then scaled-up; most experimental studies measuring productivity or ecosystem function are conducted closer to the scale of individual plants. Our study demonstrates that in *T. testudinum* beds, the assumption of a strong and invariant relationship between biomass and productivity fails at the plant level. At the scale of short shoots, the relationship between biomass and productivity is often weak and is not consistently positive (Fig. 2), suggesting that biomass is a flawed indicator of productivity.

The relationship between biomass and growth is dependent upon seagrass bed identity. A number of variables are likely to differ between beds and affect both biomass and productivity, including herbivory rate, seagrass bed size, genetic differences, epibiont growth, flow regimes, nutrient availability, and light regimes. Neither epibiont biomass nor sea urchin densities could consistently explain the difference in patterns of biomass-productivity relationships between beds (Fig. 3). Additionally, we did not measure belowground biomass in this study, which may have explained variation in

aboveground productivity between beds. *Thalassia testudinum* can differentially allocate production to either roots or shoots, but in general, allocations of energy to above- and below-ground biomass are equal (Duarte and Chiscano 1999). We did not seek to explain the mechanisms driving the patterns observed, but merely to demonstrate that the relationship between biomass and productivity is not consistent.

Many studies measure change in biomass, or growth rate, as an estimate of productivity. Yet, given any cell death or tissue loss, standing biomass will underestimate productivity. Given any variability in death rate among treatments or sites, standing biomass will estimate productivity inconsistently and potentially lead to misinterpretation of results. In the current study, long-term change in biomass drastically underestimated productivity based on short-term growth estimates (Fig. 4). Further, biomass did not consistently underestimate productivity to the same degree, since the rank order of the beds changes between long- (3 month) and short-term (1-2 weeks) growth estimates (Fig. 4). In an experimental design, the strength of this variation relative to variation among treatments must be considered and could lead to both Type I and Type II statistical errors (Sokal and Rohlf 1995).

In terrestrial systems, growth rate is often measured in the absence of consumers, which eliminates an important source of tissue loss and may reduce variability in the biomass-productivity relationship. The potential for tissue loss is greater in marine systems; herbivory is more intense (Cyr and Pace 1993) and tissue is quickly lost to wave action (Gaylord et al. 1994), potentially leading to greater variability in the relationship between biomass and productivity. However, the primary producers in marine systems (macroalgae, seagrasses, and cyanobacteria) are capable of rapid regrowth of lost biomass following disturbance or herbivory relative to terrestrial plants. Bruno et al. (2005) controlled for tissue loss in a marine macroalgal system by excluding herbivores in the field. In the laboratory, their experiments were conducted in enclosed mesocosms, such that lost tissue did not leave the closed system. Despite their efforts, Bruno et al. (2005) report negative growth estimates, suggesting that even when controlling for major sources of disturbance, tissue loss may exceed productivity.

Our results suggest that the relationship between biomass and productivity is unpredictable in seagrass beds. Despite high productivity, intrinsic limits to the size of organisms and extrinsic processes should act to buffer the change in biomass over long time scales. This is not surprising, since we do not, nor would we expect to observe 100 meter long seagrass blades. Stable climax communities may have high productivity rates, but little change in biomass over time (Odum and Odum 1955, Carpenter 1986). Yet, if productivity is measured as a change in biomass, these communities will be falsely interpreted as relatively unproductive. Previous work on the relationship between biodiversity and productivity has demonstrated inconsistent relationships between these two factors at different sites (e.g., Hector et al. 1999). However,

the majority of these studies measure productivity as biomass or change in biomass (Hooper et al. 2005). Given our results, a portion of the variance in the diversity-productivity relationship may be explained by differences in the inherent relationship between biomass and productivity at different sites and among scales and may help to explain the inconsistent results across studies.

The use of biomass or change in biomass as an estimate of productivity requires an intimate knowledge of both the system and the inherent relationship between the variable measured and productivity. Although the number of studies in aquatic systems is increasing, productivity has most often been measured in terrestrial plant communities (Hooper et al. 2005). There are likely ecological processes acting in this seagrass system that are different from those in terrestrial or other marine systems (Cyr and Pace 1993), but we believe that the similarities outnumber the differences. Each ecosystem is composed of photosynthetic primary producers and secondary consumers. Each is exposed to some level of disturbance, both biotic and abiotic, and experiences tissue or waste loss as a result. Although variation in the biomass-productivity relationship is potentially greater in marine systems relative to terrestrial systems, further studies should explore the nature of this relationship in specific ecosystems and the assumption should be tested before the method is used.

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References

- Agawin, N.S.R., Duarte, C.M., Fortes, M.D., Uri, J.S. and Vermaat, J.E. 2001. Temporal changes in the abundance, leaf growth and photosynthesis of three cooccurring Philippine seagrasses. *J. Exp. Mar. Biol. Ecol.* 260: 217-239.
- Begon, M., Townsend, C.R. and Harper, J.L. 2006. *Ecology: from Individuals to Ecosystems*. Blackwell Publishing, Malden, MA.
- Belsky, A.J., Carson, W.P., Jensen, C.L. and Fox, G.A. 1993. Overcompensation by plants herbivore optimization or red herring. *Evolutionary Ecology* 7: 109-121.
- Blanchette, C.A. 1996. Seasonal patterns of disturbance influence recruitment of the sea palm, *Postelsia palmaeformis*. *J. Exp. Mar. Biol. Ecol.* 197: 1-14.
- Bruno, J.F., Boyer, K.E., Duffy, J.E., Lee, S.C. and Kertesz, J.S. 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecol. Lett.* 8: 1165-1174.
- Bruno, J.F., Lee S.C., Kertesz, J.S., Carpenter, R.C., Long, Z.T. and Duffy, J.E. 2006. Partitioning the effects of algal species identity and richness on benthic marine primary production. *Oikos* 115: 170-178.
- Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral-reef algal communities. *Ecol. Monogr.* 56: 345-363.
- Cubit, J.D. 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65: 1904-1917.
- Cyr, H. and Pace, M.L. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361: 148-150.

- Dayton, P.K., Tegner, M.J., Edwards, P.B. and Riser, K.L. 1999. Temporal and spatial scales of kelp demography: The role of oceanographic climate. *Ecol. Monogr.* 69: 219-250.
- Downing, A.L. and Leibold, M.A. 2002. Ecosystem consequences of species richness and composition in pond food webs. *Nature* 416: 837-841.
- Duarte, C.M. and Chiscano, C.L. 1999. Seagrass biomass and production: a reassessment. *Aquatic Bot.* 65: 159-174.
- Duffy, J.E., Macdonald, K.S., Rhode, J.M. and Parker, J.D. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: An experimental test. *Ecology* 82: 2417-2434.
- Fourqurean, J.W., Willisie, A., Rose, C.D. and Rutten, L.M. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Mar. Biol.* 138: 341-354.
- Gaylord, B., Blanchette, C.A. and Denny, M.W. 1994. Mechanical consequences of size in waveswept algae. *Ecol. Monogr.* 64: 287-313.
- Gower, S.T., McMurtrie, R.E. and Murty, D. 1996. Aboveground net primary production decline with stand age: Potential causes. *Trends in Ecology & Evolution* 11: 378-382.
- Gurevitch, J., Scheiner, S.M. and Fox, G.A. 2002. *The Ecology of Plants*. Sinauer Associates, Inc., Sunderland, MA.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. and Lawton, J.H. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286: 1123-1127.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. and Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75: 335.
- Krebs, C.J. 2001. *Ecology*. Benjamin Cummings, San Francisco, CA. 5th edition.
- Menge, B.A. 1976. Organization of New England rocky intertidal community role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* 46: 355-393.
- Odum, H.T. 1959. *Fundamentals of Ecology*. W. B. Saunders Company, Philadelphia, PA.
- Odum, H.T. and Odum, E.P. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* 25: 291-320.
- Paige, K.N. and Whitham, T.G. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am. Nat.* 129: 407-416.
- Quinn, G.P. and Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- Ricklefs, R.E. and Miller, G.L. 2000. *Ecology*. W.H. Freeman and Company, New York, NY.
- Rosenzweig, M.L. and Abramsky, Z. 1993. How are diversity and productivity related? In: Ricklefs R.E. and Schluter D. (eds), *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago, IL. pp. 52-65.
- Roxburgh, S.H., Berry, S.L., Buckley, T.N., Barnes, B. and Roderick, M.L. 2005. What is NPP? Inconsistent accounting of respiratory fluxes in the definition of net primary production. *Funct. Ecol.* 19: 378-382.
- SAS Institute, Inc. 2001. JMP Version 4.0.4.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry*. W. H. Freeman and Company, New York, NY. 3rd edition.
- Tomlinson, P.B. and Vargo, G.A. 1966. On morphology and anatomy of turtle grass *Thalassia testudinum* (Hydrocharitaceae). I. Vegetative morphology. *Bull. Mar. Sci.* 16: 748-761.
- Valentine, J.F., Heck, K.L., Busby, J. and Webb, D. 1997. Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. *Oecologia* 112: 193-200.
- Williams, S.L. and Heck, K.L. 2001. Seagrass community ecology. In: Bertness, M.D., Gaines, S.D. and Hay, M.E. (eds), *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA. pp. 317-337.
- Zieman, J.C. 1974. Methods for study of growth and production of turtle grass, *Thalassia testudinum* König. *Aquaculture* 4: 139-143.

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