Interactive Effects of Diversity and Biomass on Productivity: Insights from Succession

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Abstract

Do commonly observed spatial relationships also exist over time? As an example of attempting to answer this question, this article examines whether the frequently observed diversity-biomass-productivity-relationships over space can also be seen over time. Syntheses of long-term data and literature show that when the full successional cycles are examined, diversity and productivity are usually positively related to each other but unimodally related to biomass. These relations are consistent with frequently observed patterns over space. The mechanisms underlying the spatial relationships regarding how these three variables affect each other may also apply to the temporal patterns. However, as diversity, biomass, and productivity are temporally correlated and change simultaneously with physical factors and with time, identifying any causal relationships among them would need experimental confirmation.

Introduction

Diversity and biomass are critical community components and productivity is a strong indicator of ecosystem functioning and performance. What determines species diversity in a community and what is the role of diversity in ecosystem performance are critical issues in community and ecosystem ecology (Loreau, et al. 2001; Bai et al., 2004). Previous field studies have observed positive density-diversity relationship (May, 1975) and hump-shaped relationship between biomass and diversity

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(Waide et al., 1999). Several diversity (seeding) experiments have produced positive diversity-productivity relationships. The proposed mechanisms for these relationships include interspecific facilitation and niche complementarity (over yielding) (e.g., Grime, 1973; Oksanen, 1996; Waide et al., 1999; Loreau et al., 2001). However, studies so far have examined separately the effects of biomass on diversity (field observation) or the effects of diversity on productivity (diversity seeding experiments) and numerous descriptions of diversity-productivity relationships actually used standing crop biomass data, but the interactive (or mutual) effects of all these variables on each other have not been investigated (Guo, 2007).

One of the most intriguing questions in modern ecology is whether some common spatial patterns also exist over time. Indeed, some spatial patterns or relationships have been observed over time, especially when appropriate scale is used. For example, using long-term census data of annual plants, Guo et al. (2000) found that the positive relationship between numerical abundance and distribution existed over both space and time, i. e. the species with broader spatial distribution (number of quadrats) also emerged more often over time (number of years). Adler and Lauenroth (2003) described the similarities between species-time relationship and commonly observed species-area relationship and addressed the importance of scale for comparison. Synthesizing extensive successional data, Guo (2003, 2005) concluded that the hump-shaped biomass-diversity relationship frequently observed over space was also found in succession. However, these syntheses did not include any ecosystem performance measures such as productivity; therefore the possible functions of diversity and biomass were not discussed. Also, similar to the spatial relationships, diversity, biomass, and productivity change simultaneously with physical factors (Huston 1999), making the identification of underlying mechanisms (or cause and effect) difficult, unless experimental tests or confirmation are performed.

While extensive research on interrelationships among diversity, biomass and productivity has been done spatially, better understanding of temporal patterns and relationships may be equally critically for our understanding of ecosystem functioning and management, especially when more natural habitats undergo succession due to increasingly human causes. As the measurement of productivity has a time factor, temporal data, especially successional data that cover different stages of the whole cycle might be suitable for examining the temporal relationships among diversity, biomass, and productivity. In this article, I will: ① review available succession data, especially those covering the entire cycles, ② describe how productivity, biomass, and diversity change simultaneously during succession, and ③ infer possible causal relationships among these variables and associated mechanisms from corresponding spatial patterns and proposed explanations.

1 Temporal changes in diversity, biomass and productivity in succession

Biomass is usually defined as the amount of dry organic material produced per unit of area (e.g., $g \cdot m^{-2}$) and productivity (or carbon sequestration rate) is defined as the biomass production per unit of area and time (e.g., $g \cdot m^{-2} \cdot a^{-1}$). Thus biomass and productivity are fundamentally different measures of ecosystem properties and may show different relationships with other community variables such as diversity. Because the measurement of productivity which involves a time factor and successional data usually cover temporal gradients of community variables, I use successional data to examine the relationships among diversity, biomass, and productivity. Although succession after a major disturbance may exhibit different development trajectories, I discuss the most likely scenario that fits most of the cases (Reiners, 1983; Weiner, 2001; Chen and Popadiouk, 2002).

Theory predicts that at the beginning of succession, diversity measured as species richness throughout this study increases because of colonization (both immigration and new germination which require time; see Hart and Chen 2006, 2008) and facilitation (e.g., Odum, 1969; Whittaker, 1975; Connell, 1978; Mouquet et al., 2003). Biomass also increases rapidly at the beginning and then remains relatively constant, assuming no further significant disturbances are imposed on the community (e.g., Odum, 1969; Sprugel, 1984; Bonser and Reader, 1995; Moorcroft et al., 2001). The dramatic increase in biomass (see above) in this stage is the product of high density and productivity, which occurs because there is a large base of living plant material for continuing growth and yet enough space and resources to support fast growth (Huston and DeAngelis, 1994). In the transitional or stem exclusion stage, biomass reaches an intermediate level; total plant density may be the highest at this stage because most individuals grow fast and are larger than they were at the early stage but still much smaller than in the late stages (Swaine and Hall, 1983).

Species diversity in this stage could be the highest possible because both early species and emerging late stage species coexist (Hart and Chen, 2008). In late stage (or steady state), however, the relatively constant biomass indicates a decline in productivity (e. g., Berger et al., 2004; Ryan et al., 2004). Diversity and productivity decline because most individuals of some species grow so large, and soil resources, space, and light become limited; and individuals of less competitive species die out during self-thinning and also because some individuals reach their longevity (Fig. 3 - 1; but see Ryan et al. (2004) for experimental explanations).

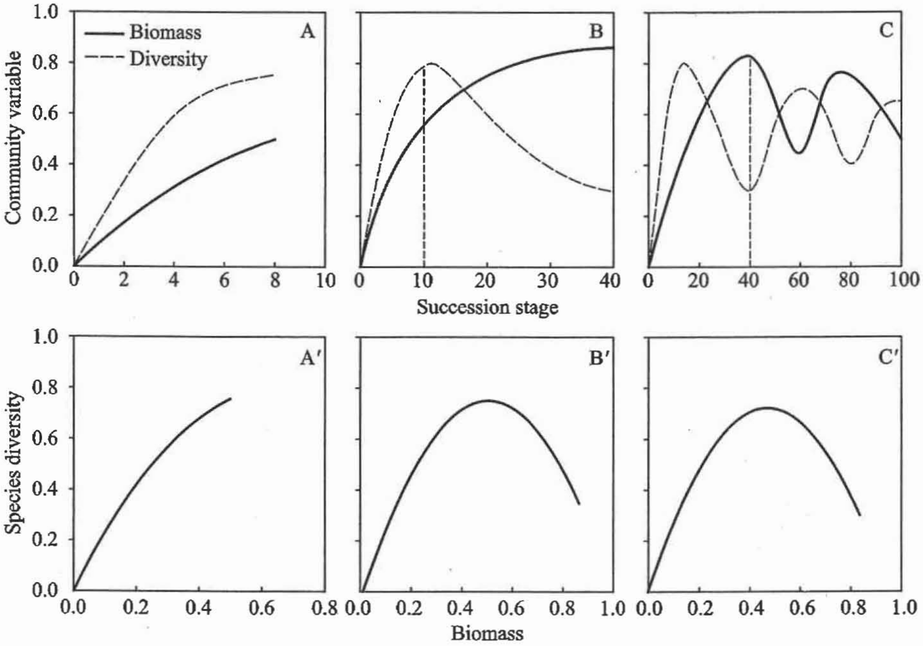

Fig. 3 - 1 Temporal dynamics of diversity and biomass and their relationships after a major disturbance. A, B, and C show the successional changes in diversity and biomass in the same ecosystem in 10, 40, and 100 years, respectively. A′, B′, and C′ show the corresponding relationships between biomass and diversity in 10, 40, and 100 years, respectively. The difference between experimental and natural communities is that in experiments, aboveground biomass is removed for measuring productivity (but belowground biomass continues to accumulate; Guo et al. 2006) so the time needed for the hump-shaped curve to occur would be longer than natural settings where both above and belowground biomass is allowed to accumulate.

2 Field data

Successional data are extensive yet most of the studies are not long enough to cover the entire successional cycle or simultaneously monitor multiple ecosystem variables. Here I present two field examples of primary succession as exceptions that covered the whole successional cycles and measured both diversity and biomass (or plant cover). One (Litcher, 1998) also actually estimated productivity and in the other (Viereck, 1966), productivity was estimated from increases of plant cover over time. Although not included in the data sets, patterns of temporal changes in total plant density may be inferred from many other successional studies (e. g., Swaine and Hall, 1983).

2.1 Primary succession on Lake Michigan sand dunes

Lichter (1998) documented patterns of primary succession across a chronosequence of stable sand dunes around northern Lake Michigan. Species diversity, basal area, aboveground biomass, aboveground litter production, proportion of full sunlight reaching the forest understory on 72 dunes, and soil properties on 20 dunes for the past 2 375 years were described using data collected from replicated survey plots. The patterns are associated with the regularity of dune formation with similar initial conditions of parent materials, topography, and species pool during development of the chronosequence.

In early succession, species diversity of open dune species, understory species, and canopy tree species all increased. After a peak of diversity at 285 years, open dune species were eliminated at ca. 800 years and understory species gradually declined while canopy tree species remained relatively constant. Biomass increased rapidly in the first 800 years then remained relatively constant. Similar to diversity, productivity (increments of biomass over time) first increased rapidly in early succession and then declined in late succession. Regressions on the long-term data revealed that biomass was unimodally related to diversity, and productivity and diversity was positively linearly related (Fig. 3-2).

2.2 Succession on Muldrow Glacier, Alaska

Viereck (1966) described plant succession and soil development in the Alaska

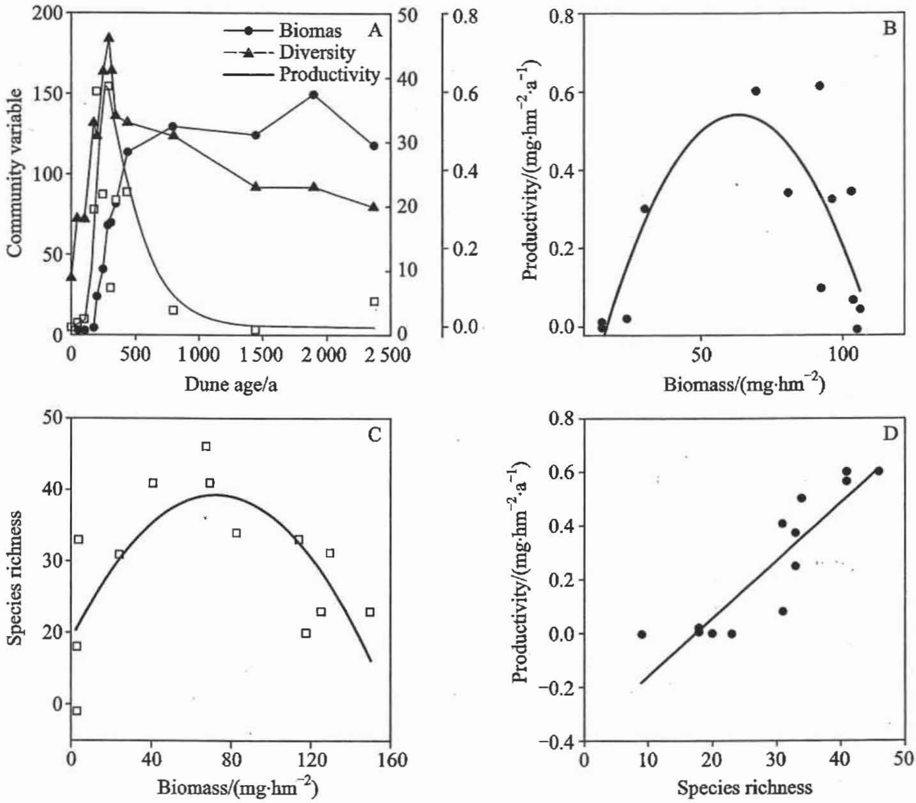

Fig. 3-2 Temporal changes in diversity, biomass, productivity (A), and their relationships (B, C, D) during long-term succession on coastal Lake Michigan sand dunes, using data from Lichter (1998). Productivity was estimated as temporal changes in biomass (B) changes, $(B_{t+1} - B_t)/a$, and the curve in (A) was the derivative of the fitted logistic model (note that the possible lose due to mortality and consumption were not included in calculation). Lichter (1998) produced similar curve of the fitted logistic model for the regression plot of ecosystem carbon (C) against estimated dune age. In panel-A, the left, right, and added y-axes represent biomass, diversity, and productivity, respectively.

Range. Succession started from completely bare outwash surface of the Muldrow Glacier. Adjacent to a climax tundra on similar parent material were four large, relatively homogeneous ecosystems in varying degrees of plant and soil development occurred on progressively younger terraces of the McKinley River. The five ecosystems comprised a chronosequence of primary succession with all independent variables relatively constant except time. The five ecosystems represented a successional sequence: pioneer stage, meadow stage, early shrub stage, late shrub stage, and climax tundra. This study did not measure biomass directly, but measured plant cover instead. The data showed that at the beginning of succession, species diversity and plant cover increased rapidly and all bare ground was covered by vegetation within 100 years. Total plant cover continued to increase until a maximum, and then remained relatively constant in the late shrub and climax stages while species diversity declined. Productivity (calculated as increments of plant cover over time) showed similar changes in diversity. Regression analyses revealed a hump-shaped relationship between diversity or productivity and total plant cover (as an estimate of biomass) and a positive relationship between diversity and productivity (Fig. 3 – 3).

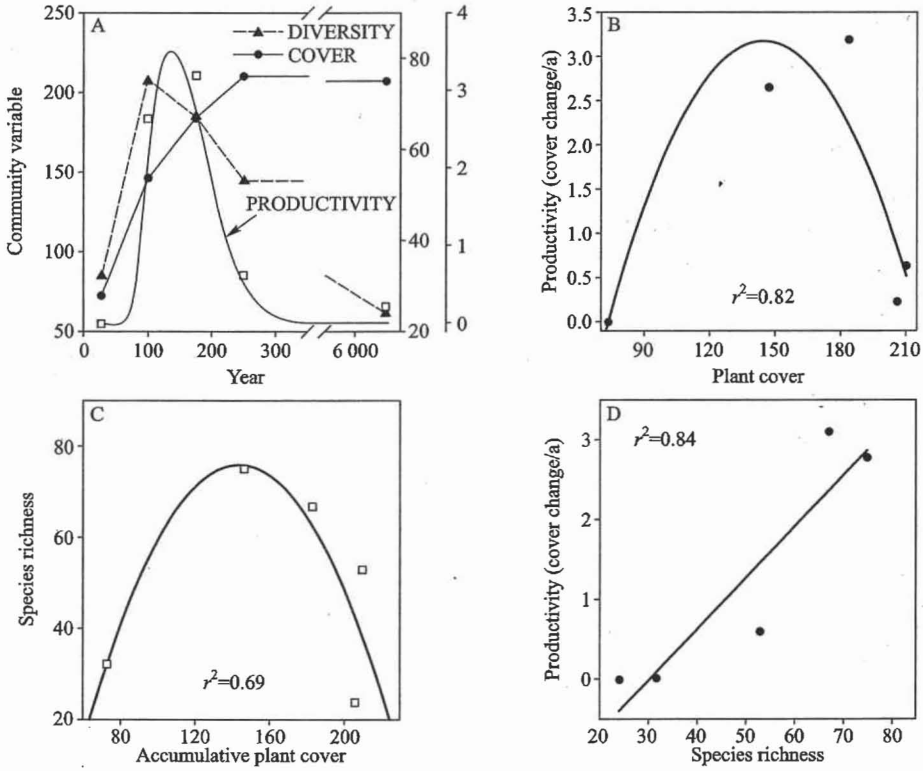

Fig. 3 – 3　Temporal changes in diversity, total plant cover (as an estimate of biomass), productivity (estimated as the increment of total plant cover over time) (A), and their relationships (B, C, D) during long-term succession on gravel outwash of the Muldrow Glacier, Alaska, using data from Viereck (1966). Successional age class, 1 = pioneer stage (25 ~ 30 a), 2 = meadow stage (100 a), 3 = early shrub stage (150 ~ 200 a), 4 = late shrub stage (200 ~ 300 a), 5 = climax stage (5 000 ~ 9 000 a). Productivity was estimated as the times of total plant cover (C) increases over time (note that the possible loss due to mortality and consumption were not included), and the curve was the derivative of the fitted logistic model. The values on the horizontal axis in B, C, D were the sums of the percent covers of all component species. In panel-a, the left, right, and added y-axes represent biomass, diversity, and productivity, respectively. For further details, see Viereck (1966).

3 Patterns in related studies

Studies that show similar patterns and support the general model presented here are numerous. For example, based on field observations on the long-term post-fire recovery of the oak-pine forest at Brookhaven, New York, Whittaker (1975) presented a successional model projecting temporal changes in species diversity, biomass, and productivity from pioneer to early forest to climax. Correlations among productivity, biomass, and diversity in his general model showed similar patterns to those reported in the above two field studies (for details, see Whittaker (1975) and literature therein).

Examples supporting the above field observational results and Whittaker's model include ① hump-shaped relationship between biomass and productivity: Möller et al. (1954), Black (1964), Noy-Meir (1975), Shidei and Kira (1977) and Begon et al. (1995); ② hump-shaped relationship between biomass and diversity: Grace 1999; and ③ positive relationships between diversity and productivity: Odum (1969) and Alldrege et al. (2001). Other studies that did not examine exactly the above relationships but showed similar temporal patterns for at least one of the three variables include: ① diversity: Connell (1978); ② biomass: Moorcroft et al. (2001); ③ productivity: Möller et al. (1954), McMurtrie et al. (1995), Gower et al. (1996), Nisbet et al. (1997), Alldrege et al. (2001), Weiner (2001) and Pan et al. (2002); ④ two of the three variables: Cooke (1967), Odum (1969), Chapman et al. (1975), Shidei and Kira (1977), Connell (1978), Southwood et al. (1979), Peet (1981), Fisher et al. (1982), Sprugel (1984), Pan et al. (2002), Ryan et al. (2004), and ⑤ all three variables: Oliver and Larson (1996).

To examine the generality of the successional patterns described in the two field examples, I conducted a literature survey on 185 published studies that examined diversity, biomass, or productivity. Among these studies, 8 (4%) examined all the three community variables, 34 (18%) examined both diversity and biomass, 4 (2%) examined both diversity and productivity, 20 (11%) examined both biomass and productivity, and the rest (119 or 64%) examined one variable only. Among the 91 studies that examined diversity (measured by species richness or Shannon-

Wiener's index), 60 (66%) showed a rapid rise to a peak in diversity right after disturbances and then the diversity dropped to the level in mature community. Among the 127 studies that examined biomass (or plant cover) 114 (90%) exhibited a rapid increase in biomass immediately after disturbances and the rate of increase then declined thereafter. Among the 38 studies that examined productivity, 28 (74%) showed patterns similar to species diversity. The rest showed either random fluctuation or no clear temporal pattern. Although the literature collected in this study could be biased by excluding many short-term studies that monitored early succession only, the majority of long-term field observations seem to show some general patterns based on Whittaker's (1975) extensive observations in terrestrial ecosystems (see also Guo, 2003).

There are several reasons that may cause the variations from the patterns described. The first is related to the concept, definition, and the measurement of the variables involved. The difference between productivity and biomass results in their distinctive relationships with diversity and possibly other variables. However, in some studies where direct measure of productivity might be difficult, productivity and biomass were either treated the same or standing biomass was used as an estimate of productivity (Aarssen 2001).

Second, similar to the spatial patterns that often depend on the scale, for the above relationships to occur, the variables must cover great or full ranges of their values from low to high (see next section). For example, in some secondary succession, the disturbance is so minor and biomass destruction is less significant thus the lower portion of the biomass range is missing. On the other hand, as more natural habitats undergo increasing human disturbances, the 'normal' recovery processes are often interrupted before climax (Oliver and Larson, 1996). In these cases, we would not be able to detect any relationship among the three variables. The two examples in this study were under somewhat 'ideal' conditions, i. e. succession started from bare ground and the communities were able to complete the full successional cycle without major disruptions (Fig. 3-1C, C').

Third, it becomes clear that we need some baseline information regarding how long it may take for a particular ecosystem type to recover from a certain level of disturbance. For example, succession in many types of forests needs hundreds of years monitoring, and yet many studies have only examined the early succession thus only positive relationships among the three variables have been observed. This could be because of the difficulties in pursuing long-term research, lack of man power, or personnel changes in investigators. Additional possible causes for the exceptions to the patterns described here are given in Guo (2003).

4 Mechanisms and comparisons with spatial patterns

In many aspects, the temporal relationships discussed above are very similar to those observed over space, especially when appropriate (mostly longer temporal) scales are used. One condition under which these patterns (or relationships) emerge is that the studies should be conducted over strong spatial (across plots) or temporal (across successional years) environmental gradients. Because diversity, biomass, and productivity simultaneously change along the successional gradients (e. g., the productivity curve in succession is very similar to overall plant density, carbon sequestration rate, and habitat quality; see Swaine and Hall, 1983; Berger et al., 2004; Ryan et al., 2004; Schulze et al., 2005), correlations among these variables cannot confirm any causal relationships. However, if relationships among the three variables indeed exist, the remarkable similarities between spatial and temporal biomass-diversity-productivity relationships suggest that the proposed mechanisms for spatial patterns may also apply to temporal patterns (e. g., through temporal niche complementarity).

In the successional process, the hump-shaped biomass-productivity relationship is easy to understand. A system in early succession is most dynamic when biomass is low, all three variables show increasing trends, leading to positive relationships. Biomass increases rapidly as a result of high productivity. In late succession, however, as individuals or the community age, resource availability declines yet matured individuals or community still need large amounts of resources for maintenance, thus making a negative contribution to productivity (e. g., Weiner, 2001). In other words, the resources (e. g., N, P) allocated to maintenance after the community matures cannot be allocated to further growth (e. g., Vitousek and Reiners, 1975). In this stage, biomass passes a certain level and both diversity and productivity decline, resulting in negative correlations of diversity or productivity with biomass, and the cause of productivity decline with age may be at least partly due to resource limitation. If the positive diversity-productivity relationships in experimental communities are confirmed, the declined diversity in late succession may also in part be responsible for the decline in productivity.

Previously proposed mechanisms for the hump-shaped biomass-diversity relationship include colonization/facilitation and competitive exclusion (e. g., Grace, 1999). Yet, these mechanisms and physical factors may co-operate simultaneously, are interrelated, and thus are mutually responsible for the observed relationships among diversity, biomass, and productivity, and only the relative importance may change with time and space. The possible effects of density on the diversity-productivity relationship also need attention (He et al., 2005). For example, in late succession when biomass reaches a high value, many pioneer species disappear and the number of individuals (density) of remaining species decline due to the individual longevity and continuing "self-thinning" (e. g., Swaine and Hall, 1983). The logic of the relationships among diversity, biomass, and productivity may also be explained by looking at the reverse order of succession. When a homogeneous landscape with mature (climax) vegetation is disturbed at different magnitudes and frequency over space, it first becomes patchy or heterogeneous, and the habitat would loss its highest potential biomass due to the material lose in disturbed patches. Yet, the disturbed habitats with lesser biomass would leave more space for higher diversity therefore higher productivity.

The previously claimed scale issue (e. g., Waide et al., 1999) is highly relevant to both biomass-diversity and biomass-productivity relationships but may be less to the diversity-productivity relationship. Similar to earlier work on spatial analyses, scale is also an essential factor in temporal patterns (e. g., Adler and Lauenroth, 2003; Guo, 2003). Successional data at one location but across different successional stages provide a unique and ideal opportunity for examining temporal relationships among diversity, biomass, and productivity. A critical requirement in using successional or any other temporal data to examine these relationship is that the gradient or the ranges of community variables must be broad enough to cover the extreme low (i. e. right after disturbance) and high levels of biomass (e. g., biomass in a mature community; see also Chalcraft et al., 2004). Furthermore, the ideal diversity measures should include all species rather than a subset of species (e. g., trees).

5 Conclusions

Long-term data show that, during succession, diversity is unimodally related to biomass and productivity is positively related to diversity but unimodally related to biomass. In many aspects, these temporal relationships resemble those observed over space. However, the underlying mechanisms are the major challenge ahead. The effects of physical factors on diversity, biomass, and productivity and their relationships need further investigation. It is also crucially important to make clear distinctions between productivity and biomass, and between causal and response variables in describing their relationships with diversity. Incorporating spatial and temporal patterns as well as experimental studies in the target systems may greatly improve our understanding of the ecosystems functions of biodiversity and decision making for ecosystem management and restoration (Adler and Lauenroth, 2003; Bai et al., 2004; Ryan et al., 2004).

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