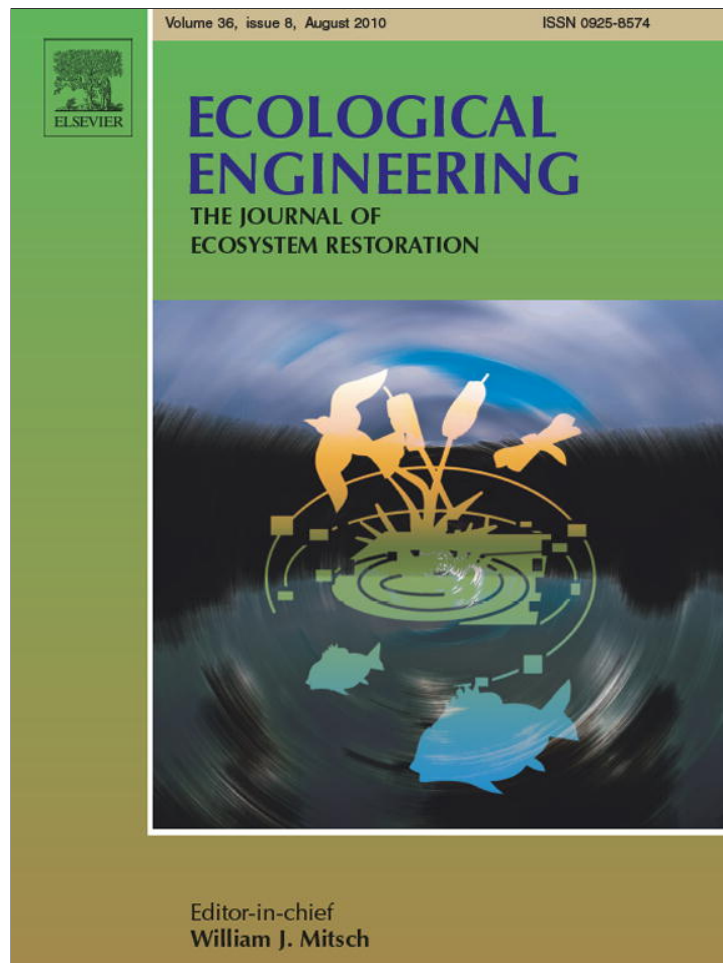


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Ecological stoichiometry explains larger-scale facilitation processes by shrubs on species coexistence among understory plants

Takehiro Sasaki^{a,*}, Yu Yoshihara^b, Undarmaa Jamsran^c, Toshiya Ohkuro^d

^a Graduate School of Life Sciences, Tohoku University, 6-3 Aoba, Aramaki, Aoba-ku, Sendai 980-8578, Japan

^b Kawatabi Integrated Field Science Center, Graduate School of Agricultural Science, Tohoku University, Kawatabi, Naruko-onsen, Osaki 989-6711, Japan

^c Center for Ecosystem Study, Mongolian State University of Agriculture, 210153 Ulaanbaatar, Mongolia

^d Department of Ecosystem Studies, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

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ABSTRACT

Plant facilitation (positive plant–plant interactions) strongly influences biodiversity, structure, and dynamics in plant communities, and the topic has received considerable attention among ecologists. Most studies of facilitation processes by shrubs have been conducted at small spatial scales between shrubs and their neighboring species. Yet, we know little about whether facilitation processes by shrubs at a small scale (i.e., a patch scale) also work at a larger scale (i.e., a site scale) in terms of the maintenance of biodiversity. Here, we report that the facilitative effects of shrubs on plant diversity at a larger scale can be explained by changing ecological stoichiometry. The soil fertility showed unimodal shape along shrub cover gradient, suggesting that the facilitative effects of a shrub do not necessarily increase as the shrub develops. The unimodal shape of dependence of plant species richness on shrub cover probably was generated by the unimodal dependence of soil fertility on shrub cover. Soil nutrient enrichment by shrubs shifted low N:P ratios of plant communities with low levels of shrub cover to more balanced N:P ratios at intermediate levels of shrub cover. At the peak N:P ratio along the gradient in shrub cover, the maximum species richness and functional richness were observed, which was consistent with the unimodal relationship predicted by the resource balance hypothesis. Thus, our findings showed that facilitation processes by shrubs at a patch scale also work at a larger scale in terms of the maintenance of biodiversity. Because observed larger-scale facilitation processes are enhanced at some intermediate levels of shrub cover, this study offers practical insight into the need for management practices that allow some intermediate levels of grazing by livestock for optimizing the role of larger-scale facilitation processes in the maintenance of biodiversity and ecosystem functioning in arid and semi-arid rangelands.

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1. Introduction

Plant facilitation (positive plant–plant interactions) strongly influences biodiversity, structure, and dynamics in plant communities. The topic has received considerable attention among ecologists in the last two decades, and plant facilitation is now widely recognized (Callaway, 1995; Bruno et al., 2003; Padilla and Pugnaire, 2006; Brooker et al., 2008). Typical examples are evident in harsh, limiting environments, particularly arid ecosystems, where some shrub species ameliorate the abiotic conditions in some way (Shachak et al., 1998; Shumway, 2000; Facelli and Temby, 2002; Wright et al., 2006) or prevent herbivory (Rebollo et al., 2002), thereby providing more suitable habitats for under-

story plant species. Studies of such plant facilitation can have a practical side when applied to ecological restoration (Padilla and Pugnaire, 2006), and the findings can also be related to some of the most important current ecological issues, including the relationship between biodiversity and ecosystem functioning and the impacts of global change (Hooper et al., 2005; Brooker, 2006; Brooker et al., 2008).

Many arid ecosystems are limited by a lack of resources, particularly water and nutrients (Gutierrez and Whitford, 1987; Shachak et al., 1998). Shrub establishment increases the content of fine soil particles, seed density in the soil, and the accumulation of organic carbon and nitrogen and decreases pH in proximity to the shrubs (Shachak et al., 1998; Shumway, 2000; Facelli and Temby, 2002; Su and Zhao, 2003; Zhao et al., 2007). Once established and growing, shrubs gather sand and finer particles around them, forming mounds, and the further modification of the abiotic environment (especially soil nutrients and particle structures) by these mounds

* Corresponding author. Tel.: +81 22 795 6698; fax: +81 22 795 6699.
E-mail addresses: sasa@m.tains.tohoku.ac.jp, sasa67123@gmail.com (T. Sasaki).

(Shachak et al., 1998; Shumway, 2000) may enhance biodiversity (Maestre and Cortina, 2005; Wright et al., 2006). Most studies of such facilitation processes by shrubs have been conducted at a small spatial scale, between shrubs and their neighboring species (Shumway, 2000; Su and Zhao, 2003; Maestre and Cortina, 2005; Smit et al., 2007; Zhao et al., 2007). These studies have generally indicated that species richness of understory plants is related to the size of the individual shrubs according to a simple power relationship for a wide array of species (Maestre and Cortina, 2005; Zhao et al., 2007). Yet, we know little about whether facilitation processes by shrubs at a small scale (i.e., a patch scale) also function at a larger scale (i.e., a site scale) in terms of the maintenance of biodiversity.

Here, we report that larger-scale facilitation processes by shrubs on species coexistence of understory plants can be explained by ecological stoichiometry, the balance of multiple chemical substances in ecological interactions and processes (*sensu* Sterner and Elser, 2002). Soil nutrient amelioration by shrubs at a larger scale might affect the ratio of nitrogen to phosphorus concentrations (N:P ratio) of plant biomass at a larger scale, which can be used as an indicator of N or P limitation in plant communities (Güsewell and Koerselman, 2002; Güsewell, 2004; Güsewell et al., 2005). The resource balance hypothesis (*sensu* Braakhekke and Hooftman, 1999) predicts that in vegetation with high (P limited) or low (N limited) N:P ratios, fertilization creating a more balanced supply of N and P could increase species richness, at least if biomass production remains sufficiently low so that light does not become the single limiting resource. Interspecific differences in the acquisition or use of particular elements as well as variation in resource availability may cause coexisting species to be limited by different nutrients and thus enhance species richness (Braakhekke and Hooftman, 1999; Güsewell et al., 2005).

Given the N-limited nature of arid ecosystems, we predicted that nutrient enrichment by shrubs at a larger scale would shift from low N:P ratios of plant communities to more balanced, intermediate N:P ratios, where the maximum species richness would be observed. However, although the facilitative effects of a shrub generally increase as the shrub develops, after a certain point of development the effectiveness may diminish due to competition for light and other resources (Reisman-Berman, 2007). Therefore, to fully examine the effectiveness of larger-scale facilitation processes by shrubs, we need to assure the full variations in shrub cover appeared within a given area.

In the present study, we addressed the following questions to determine larger-scale facilitation processes by shrubs on species coexistence among understory plants. How does the variation in shrub cover relate to the modification of the soil environment and biodiversity (species richness and functional richness)? How does the modification of the soil environment by shrubs relate to N:P ratios of plant communities? Is there a unimodal relationship between N:P ratios of plant communities and biodiversity, as predicted by the resource balance hypothesis?

2. Materials and methods

2.1. Study area

The study area was situated near Mandalgobi (45°46'N, 106°16'E) in Mongolia's Dundgobi Province. The study area has long been grazed by domestic livestock under nomadic or semi-nomadic patterns of land use, and it is located in the steppe ecological zone. The main type of livestock in the area is sheep. The region's climate is arid and cold, with a short summer. Based on meteorological data provided by Mongolia's Institute of Meteorology and Hydrol-

ogy, Ministry of Nature and Environment, annual rainfall averaged 170 mm (coefficient of variation = 28%) between 1993 and 2003. Peak rainfall occurred in July, and summer and winter temperatures averaged around 19° and -14°C. The soil is sandy and the landform consists of gently sloping hills (generally less than 1.5°). Vegetation within the area is characterized by a mixture of patchily distributed shrubs and understory plants. Soil nutrients, especially nitrogen and phosphorus, are generally dispersed by wind erosion in this landscape (Sasaki et al., 2008). Consequently, plant communities might primarily be limited by these two nutrients. The predominant shrub, *Caragana microphylla*, is a nitrogen-fixing legume (Su and Zhao, 2003), which may have facilitative effects on understory herbs through soil nutrient amelioration. Nomenclature in this paper follows that of Grubov (1982).

2.2. Site selection and cross-scale patterns of facilitation by shrubs

Because it is often difficult to delineate spatial ranges differing in shrub densities at the ground level, we roughly delineated the ranges using remote-sensing techniques (Yoshihara et al., unpublished manuscript). Based on the delineation of the study area, we selected 15 sites (50 m × 50 m) with different shrub densities. To reduce spatial autocorrelation between the sites, the distances between sites were at least 1 km. Because facilitative effects of shrubs on the coexistence of understory plants are often confounded with the effects caused by grazing processes (Smit et al., 2007), we selected sites where the grazing impacts appeared to be very small, based on dung frequency within the sites (Yoshihara et al., unpublished manuscript).

Our previous work (Yoshihara et al., unpublished manuscript) demonstrated the patterns of facilitation by shrubs on species richness at three nested spatial scales within each site: 5 m × 5 m, 20 m × 20 m, and 50 m × 50 m. Results suggested that the facilitative effect of shrubs on plant species richness depended on the spatial scale, and that the effect was most pronounced at the 50 m × 50 m (Yoshihara et al., unpublished manuscript). In the present study, we focused on the underlying processes which generate the pattern at the larger scale using ecological stoichiometry.

2.3. Plant and soil sampling

In August 2008, we measured major and minor axes of all shrub individuals within each 50 m × 50 m site. We recorded the total number of all plant species appeared within 50 m × 50 m site (i.e., species richness within a site). We laid out 10 plots (1 m × 1 m) that were systematically and widely distributed within each site and sampled all aboveground standing plant materials in each plot. Plant materials within each plot were dried to constant mass and ground in a mill to form one composite sample per site. The samples were then analyzed for N and P concentrations; N was determined by the Kjeldahl method and P by the molybdovanadate method (Allen, 1989).

We also collected five pairs of on-mound and off-mound (at least 2 m from the mound) soil samples at 0–5-cm depth from randomly selected shrub individuals, for a total of 10 soil samples per site. Soil samples were combined into one composite on-mound and one composite off-mound sample per site and were subjected to the following chemical analyses (Sparks, 1996): soil pH in water (soil:solution = 1:2.5, using deionized water); organic carbon (OC, Walkley-Black); N (Kjeldahl); and available P (Bray and Kurtz). Soil texture was determined following the criteria of Spaargaren (1994).

Table 1
Plant functional traits and their categories used in the analyses. Multiple membership means that some species belong to more than one trait category.

Plant functional trait	Trait categories	Multiple membership
Growth form	Grass; forbs; subshrubs (woody just at the base); shrubs	No
Life history	Annual; biennial; herbaceous perennial; woody	Yes
Lateral spread	Erect (solitary); tussock; branched; prostrate	Yes
Phylogenetic group	Monocotyledon; dicotyledon	No
Leaf margin	Entire; toothed; revolute; thorny	Yes
Leaf shape	Linear; lanceolate; elliptic; ovate or obovate; oblong; round	Yes
Leaf form	Entire; lobed; pinnatisect; pinnate; multipinnate	Yes
Leaf attachment	Opposite; alternate; decussate; fasciculate	Yes

2.4. Data analysis

We calculated the canopy size of each shrub individual by substituting the major and minor axes into the formula for an ellipse. We summed these values within each site to obtain the shrub cover (percent) per site. In the following analyses, we used the shrub cover per site to represent the origin of larger-scale facilitation processes on species coexistence among understory plants.

To examine the relative importance of functional complementarities in species coexistence potentially promoted by the facilitative effects of shrubs, we included functional richness as well as species richness in the analyses. Here, functional richness refers to the number of functional groups, which were defined from a combination of eight plant functional traits that are considered key to determining plants' role in the functioning of the studied system (a total of 31 categories across traits; Table 1).

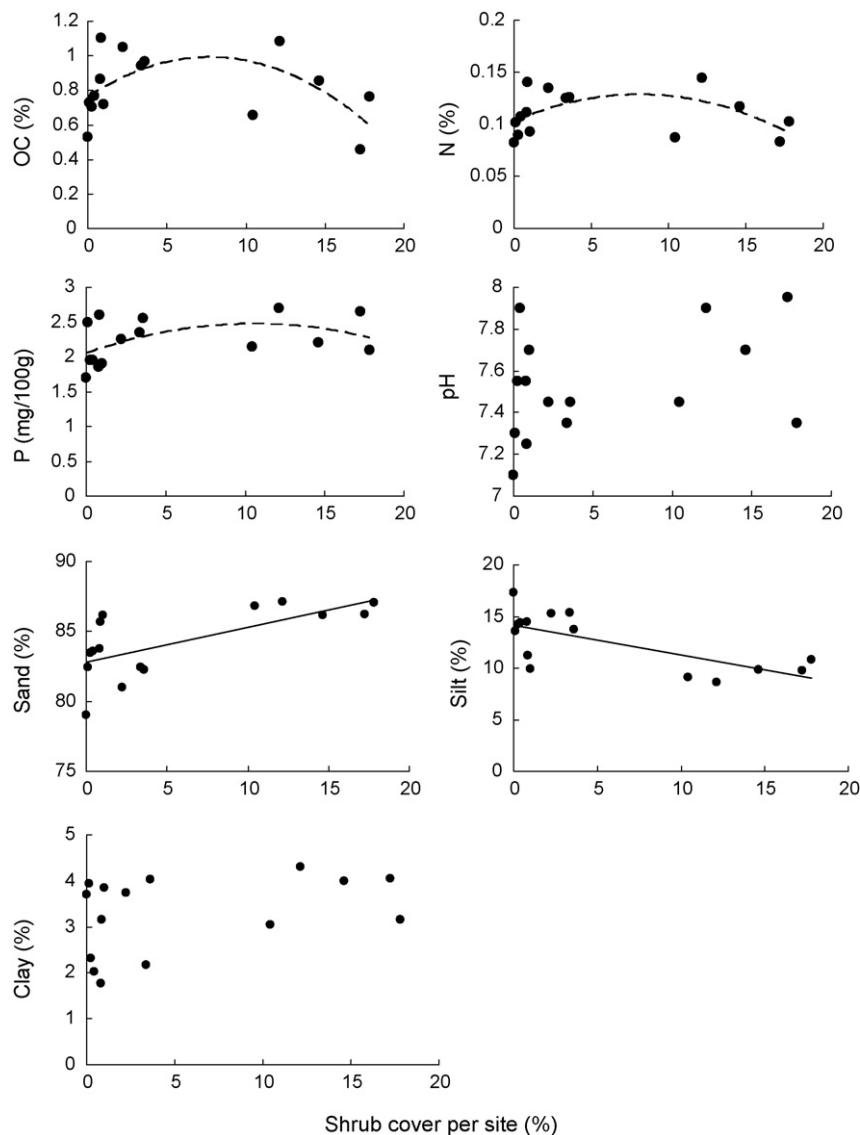


Fig. 1. The relationships between shrub cover per site and organic carbon (OC), nitrogen (N), available phosphorus (P), soil pH, sand content, silt content, and clay content. A solid line indicates a significant relationship ($P < 0.05$), whereas a broken line indicates a weak but nonsignificant trend. No line is depicted when there is no discernible pattern (i.e., relatively low R^2 values in both linear and quadratic regressions).

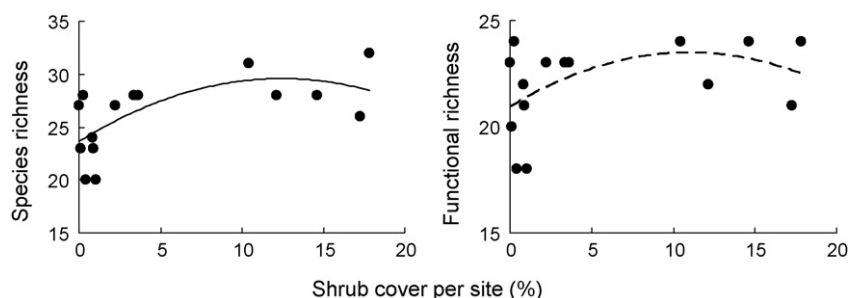


Fig. 2. The relationships between shrub cover per site and species and functional richness. A solid line indicates a significant relationship ($P < 0.05$), whereas a broken line indicates a weak but nonsignificant trend.

Soil parameters (OC, N, P, soil pH, and sand, silt, and clay contents; mean values of on-mound and off-mound samples in each site) and species and functional richness were individually regressed against the shrub cover per site, in both linear and quadratic models. If both models revealed a significant relationship, they were compared using Akaike's information criterion. We then determined the relationship between shrub cover and biomass N:P ratio and those between biomass N:P ratio and species and functional richness by the same procedure. All statistical analyses were performed with the R software (version 2.7.0, R Development Core Team, 2008).

3. Results

There were weakly unimodal, nonsignificant relationships between shrub cover and soil OC ($F_{2,12} = 2.33$, $R^2 = 0.28$, $P = 0.13$), N ($F_{2,12} = 1.74$, $R^2 = 0.23$, $P = 0.21$), and P ($F_{2,12} = 1.63$, $R^2 = 0.21$, $P = 0.23$; Fig. 1). Sand content increased significantly ($F_{1,13} = 10.99$, $R^2 = 0.46$, $P < 0.05$), whereas silt content decreased significantly ($F_{1,13} = 12.54$, $R^2 = 0.49$, $P < 0.05$) with an increase of shrub cover. Soil pH and clay content did not show a discernible pattern (i.e., relatively low R^2 values in both linear and quadratic regressions). Shrubs cover and species richness showed a significant unimodal relationship ($F_{2,12} = 4.44$, $R^2 = 0.43$, $P < 0.05$; Fig. 2), whereas the relationship between shrub cover and functional richness was weakly unimodal but nonsignificant ($F_{2,12} = 1.56$, $R^2 = 0.21$, $P = 0.25$).

There was a significant unimodal relationship between shrub cover and the biomass N:P ratio ($F_{2,12} = 4.43$, $R^2 = 0.43$, $P < 0.05$; Fig. 3). The relationship between the biomass N:P ratio and species richness tended to be unimodal, but not significant ($F_{2,12} = 3.61$, $R^2 = 0.38$, $P = 0.06$). The relationship between the biomass N:P ratio and functional richness showed a significant unimodal relationship ($F_{2,12} = 4.58$, $R^2 = 0.43$, $P < 0.05$; Fig. 4).

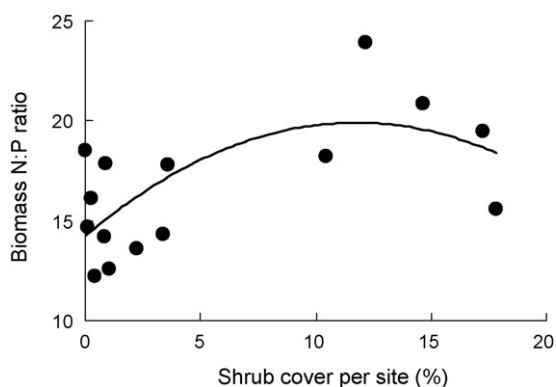


Fig. 3. The relationship between shrub cover per site and biomass N:P ratio, which showed a significant unimodal relationship ($P < 0.05$).

4. Discussion

Although we did not detect significant relationships between shrub cover and soil OC, N, and P, there was a trend of a soil nutrient amelioration effect by shrubs at the larger scale (Fig. 1). However, the relationship between each nutrient and shrub cover tended to be unimodal, suggesting that the facilitative effects of shrubs do not continually increase with shrub development. Reisman-Berman (2007) demonstrated that the effectiveness of facilitation eventually diminishes due to competition for light and other resources at a later growth stage of shrubs. In our case, we suggest that the decreasing trends of these soil nutrients with higher shrub cover probably resulted from the increase of sand content and the concomitant decrease of silt content (Fig. 1). As the shrub mounds grow, shrubs gather more sand around them, and consequently the overall soil texture of a site can shift to be coarser (Shachak et al., 1998; Shumway, 2000). Coarse-textured soil generally has poor water and nutrient retention and a high water infiltration rate (Ekwoanya and Ojanuga, 2002). Therefore, the positive aspects of the chemical modification of the soil environment by shrubs might be offset by the negative aspects of the physical modification when the shrub density within a given area is excessively high.

The unimodal relationships between shrub cover and species richness and functional richness probably reflected the unimodal trends of soil nutrient amelioration by shrubs at the larger scale. However, the percent shrub cover at which the peak species and functional richness occurred differed from the values at which the peak OC, N, and P levels occurred (Figs. 1 and 2). In our study site, facilitative processes by shrubs on species coexistence of understory plants might be largely due to the promotion of seed-trapping and subsequent seedling establishment (Shumway, 2000; Facelli and Temby, 2002; Padilla and Pugnaire, 2006), in addition to the nutrient enrichment created by shrub mounds (Shachak et al., 1998; Shumway, 2000; Facelli and Temby, 2002). The appropriate balance of two factors might be required to promote the coexistence of multiple species, thus resulting in the observed lag between the percent shrub cover values for soil nutrient peaks and those for biodiversity peaks. Such a balance also might be reflected in the difference between the percent shrub cover values for soil nutrient peaks and that for the biomass N:P ratio peak (Fig. 3).

As predicted, soil nutrient enrichment by shrubs shifted low N:P ratios of plant communities with low levels of shrub cover to more balanced N:P ratios at intermediate levels of shrub cover (Fig. 3). Again, however, when the shrub density within a given area is excessively high, soil becomes more coarse-textured with poor nutrient retention. Consequently, biomass N:P ratios decreased toward extreme values of shrub cover, indicating N-limitation in plant communities. At the peak N:P ratio (~ 20 ; Fig. 3) along the gradient in shrub cover, the maximum species richness and functional richness were observed (Fig. 4). This result was consistent with the unimodal relationship predicted by the resource balance

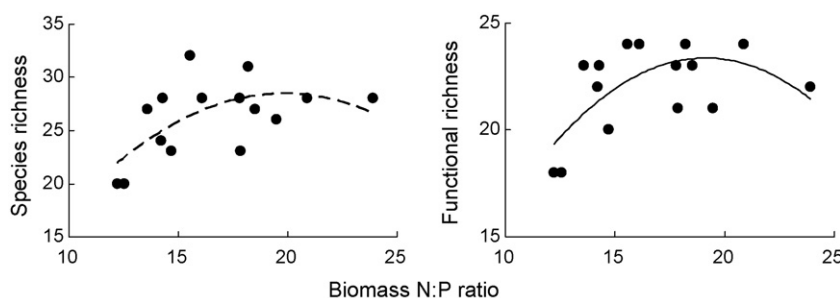


Fig. 4. The relationships between biomass N:P ratio and species and functional richness. A solid line indicates a significant relationship ($P < 0.05$), whereas a broken line indicates a weak but nonsignificant trend.

hypothesis (Braakhekke and Hooftman, 1999): species richness was maximum at intermediate N:P ratios, decreased toward lower N:P ratios, and decreased toward higher N:P ratios. Differences in the acquisition or use of particular elements among species whose seedling establishment is promoted by shrubs (Gomez-Aparicio et al., 2005), as well as spatial heterogeneity in resource availability created by shrubs at a landscape scale (Facelli and Temby, 2002; Gomez-Aparicio et al., 2005), may cause coexisting species to be limited by different nutrients and thus enhance species richness (Braakhekke and Hooftman, 1999; Güsewell et al., 2005). Although the unimodal pattern of species richness versus biomass N:P ratios was not significant, the similar unimodal pattern of functional richness versus N:P ratios was significant (Fig. 4), suggesting the relative importance of functional complementarities in species coexistence under a balanced supply of limiting nutrients (Hooper, 1998; Loreau, 1998).

A limitation of our study was that due to the potential correlation between the site identity (e.g., land use history) and soil parameters measured, we could not distinguish the effects of soil nutrient enrichment caused by shrubs from those caused by other potential factors. Despite the small possibility for the potential effect caused by the site identity on plant diversity because there were no significant differences in dung density between the sites (Yoshihara et al., unpublished manuscript), we need more controlled studies in which the shrub densities are manipulated within the same soil condition to better examine the proposed facilitation processes here. Another caveat is that other potential factors such as competition for light and other resources may also be critical to explain the changes in facilitative effects (Reisman-Berman, 2007) because soil nutrient is not the single limiting resource. In future studies, however, we need to examine the relative importance of these limiting factors for the comprehensive understanding of larger-scale facilitation processes by shrubs.

In the present study, we showed that facilitation processes by shrubs at a small scale also function at a larger scale in terms of the maintenance of biodiversity. However, our findings suggested that facilitative effects are not necessarily related linearly to shrub cover within a given area, and that larger-scale facilitation processes are enhanced at some intermediate levels of shrub cover (i.e., a more balanced N:P ratio of plant communities was observed at intermediate levels of shrub cover). Although this study was not designed to examine herbivory by livestock, our results do offer some practical insight into management procedures, such as allowing intermediate levels of grazing (Sasaki et al., 2009) in order to optimize the role of larger-scale facilitation processes in the maintenance of biodiversity and ecosystem functioning in arid and semi-arid rangelands. Our study will also provide guidance for ecological restoration of degraded shrublands in the region. Transplanting shrubs at larger scales and higher densities could potentially control nutrient loss caused by wind erosion and thereby improve

vegetation restoration. Again, however, such efforts should consider the possibility that increasing shrub density beyond some intermediate levels may actually have adverse effects on diversity because the positive aspects of soil nutrient amelioration by shrubs might be offset by the negative aspects of the physical modification when the shrub density is excessively high.

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