Working Group Report – Post-ASM (2006)
Effects of N-fixing Plants on Diversity and Relative Abundance

TITLE: Effects of N-fixing Plants on Diversity and Relative Abundance
FOLLOW-UP MEETING ORGANIZERS: Jennifer Follstad Shah, Joe Fargione
MEETING DATE: May 2007
LOCATION: Sevilleta LTER Biological Field Station, New Mexico

PARTICIPANTS PRESENT AT MEETING 1 (LTER site, affiliation): Jennifer Follstad Shah (SEV, Duke University), Joe Fargione (SEV & CDR, Purdue University[1]), Sarah Emery (KBS, Rice University[2]) Elsa Cleland (NCEAS), Isabel Ashton (NWT, University of California-Irvine), Marko Spasojevic (NWT, University of California-Irvine), Erica Smithwick (University of Wisconsin-Madison[3])

BACKGROUND: The mechanisms influencing species coexistence are poorly understood for most ecosystems. Plants with nitrogen-fixing symbionts increase inputs of nitrogen (N) to ecosystems. These plants have been shown to increase soil fertility [1, 2] and to increase tissue N [3, 4] and photosynthetic rates [4] in neighboring plants. However, it is unknown (1) whether N-fixing plants promote increased community diversity by facilitating the coexistence of neighboring plants competing for N; or (2) whether N-fixing plants generally influence community structure by favoring certain functional groups or species traits. Global change is causing predictable shifts in legume abundance. The abundance of N-fixers has been shown to decline in response to elevated N fertilization [5]. Given recent and projected global increases in nitrogen deposition, it is important to better understand the role N-fixers play in structuring native plant communities under ambient rates of N deposition.

The objective of the proposed follow-up working group were to synthesize LTER and non-LTER datasets across plant communities (grassland, cropland, and upland and riparian forests) in order to address several questions regarding the effect of N-fixers on plant community diversity and relative abundance:

Across successional grassland, cropland, and forest communities that have experienced disturbance

1. Are there predictable patterns of N-fixer abundance through successional time (e.g., high N-fixer abundance following disturbance but declining through time)?
2. Does N-fixer presence facilitate diversity and/or evenness through successional time (by increasing soil N availability and heterogeneity)?

Across natural grassland and riparian communities

1. How does the presence or absence of N-fixers influence species richness and evenness? Is the effect of individual N-fixers or N-fixers as a group significantly different from other species or functional groups (e.g. C3 or C4 grasses, non-legumes)?
2. How does the relative abundance of N-fixers affect species richness and evenness? Is the relative abundance of N-fixers correlated with the relative abundance of other functional groups?
3. Does community composition change as a function of N-fixer relative abundance? Does community composition change in the same manner and to the same degree when the relative abundance of other functional groups (e.g., C3 or C4 grasses, non-legumes) is the predictor variable?

FOLLOW-UP MEETING GOALS: Goals of this follow-up meeting included (1) compilation and synthesis of LTER and non-LTER datasets on functional group (N-fixer, C3 grass, C4 grass, non-leguminous plants) presence/absence and relative abundance and (2) development of cross-site comparative manuscripts.

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RELEVANT DATABASES: We used 5 databases for answering workshop focus questions.

Successional Dynamics on a (old-field) Repeated Chronosequence: In 1983, 100 permanent 0.5 m^2 plots were established along four parallel 80 m long transects in each of 22 fields at Cedar Creek Natural History Area (CDR) [6]. Fields ranged in age from 1 to 56 years [7]. All 2200 plots have been sampled every 5 or 6 years from 1983-2006. Plants within each plot were identified to species and their cover was estimated for each sampling date [8].

KBS019: Aboveground Net Primary Production: This dataset includes 11,510 records of annual peak aboveground plant biomass in 6 replicate early successional fields (T7), 6 replicate never-tilled old fields (T8), and 3 replicate older successional fields (SF) at Kellogg Biological Station (KBS). Five 1 m^2 sampling plots were established in each field. These plots have been measured for 10 to 15 years since 1989.

Re-establishment of Vegetation after the Yellowstone Fire of 1988: This dataset includes information from several studies. Species richness, cover by functional group, and cover of *Lupinus argenteus* were measured from 1990-1993 [9], 1996, and 2000 [10] within > 700, 1 x 10 m plots in 9 crown-fire patches (3 locations, 3 sizes). Cover by functional group and of *L. argenteus* within 3 other 1 km^2 grids also were sampled from 1989-1992 [11]. Another study recorded species richness and relative abundance within 90 widely distributed 0.25-ha plots, all within the 1988 burned area, in 1999 and 2003 [12].

Fertsyn: This dataset includes 28,368 records, representing the 784 species responses to fertilization. Plot-level relative abundance of individual species has been compiled from 10 sites (9 LTER sites plus Jasper Ridge Biological Station) and 37 experiments. Observations within the dataset date from 1982-2005.

USGS Woody Riparian Plants of the Western US: This dataset includes presence/absence and relative cover of 44 woody riparian plant species (> 1.5 m tall) along 475 stream reaches of 17 western states. Each study reach was located near a U.S. Geological Survey gaging station that had daily discharge data for at least 20 years between 1965 and 1994. Measures were collected once at each site. Data were compiled between 1997 and 2002.

RESULTS:

Across successional grassland, cropland, and forest communities that have experienced disturbance

We asked whether there are predictable patterns of N-fixer abundance through successional time (i.e., years since disturbance). We found opposing patterns in N-fixer abundance at KBS and CDR. Early successional fields at KBS had an increase in legume cover through time, while cover of N-fixers decreased at CDR through time. Preliminary results suggested that N-fixer abundance had also increased across the Yellowstone datasets through time.

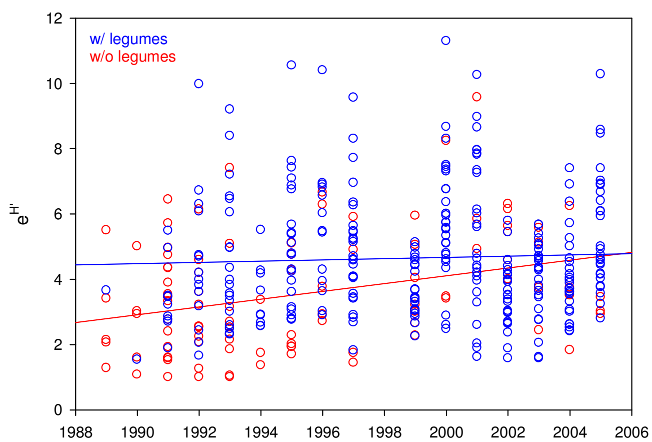

Figure 1. Evenness ($e^{H'}$) of plant diversity within plots at Kellogg Biological Station LTER from 1989-2005. Plots that included N-fixers (legumes) are shown in blue, while plots lacking N-fixers are shown in red. Plots that contained N-fixers had greater diversity through time than plots lacking N-fixers (*P* = 0.002). Diversity increased over time in plots lacking N-fixers, but not in plots containing N-fixers (*P* = 0.029). It took approximately 16 years for plots without N-fixers to achieve the same diversity present in plots with N-fixers.

Soil N availability increased at both KBS and CDR through time, despite differences in temporal patterns of N-fixer relative abundance. We postulated that increased soil N availability associated with the presence of N-fixers would promote increased species richness evenness. We found that species richness at KBS and CDR was indeed higher in plots that included N-fixers. Evenness also was greater through time at KBS in plots that included N-fixers relative to those lacking N-fixers (Fig. 1). We are still analyzing patterns of soil N availability and species richness and evenness across the Yellowstone datasets.

Across natural grassland and riparian communities

We analyzed data for control plots within 17 fertilization experiments included in the Fertsyn database and across all the plots included in the USGS database. The presence of N-fixers in natural grassland and riparian communities were correlated with higher species richness (paired-t = 3.54, p = 0.0025; Fig. 2a) and diversity (paired-t = 4.41, p = 0.0004; Fig. 2b) but similar evenness (data not shown) as compared to plots without N-fixers.

We were interested in determining whether one or a few N-fixers were driving these patterns. The effect on species richness was significantly greater than the addition of 1 additional species (null hypothesis) for just 2 of the 8 N-fixers included in the USGS database. Across N-fixers in the USGS database, the difference in species richness in plots with vs. without a N-fixing species was not significantly greater than 1 (t = 0.516, p = 0.67). We are currently conducting similar analyses for selected studies within the Fertsyn database. In addition, we plan to compare patterns for N-fixers to those for other functional groups (C3 and C4 grasses, non-leguminous forbs).

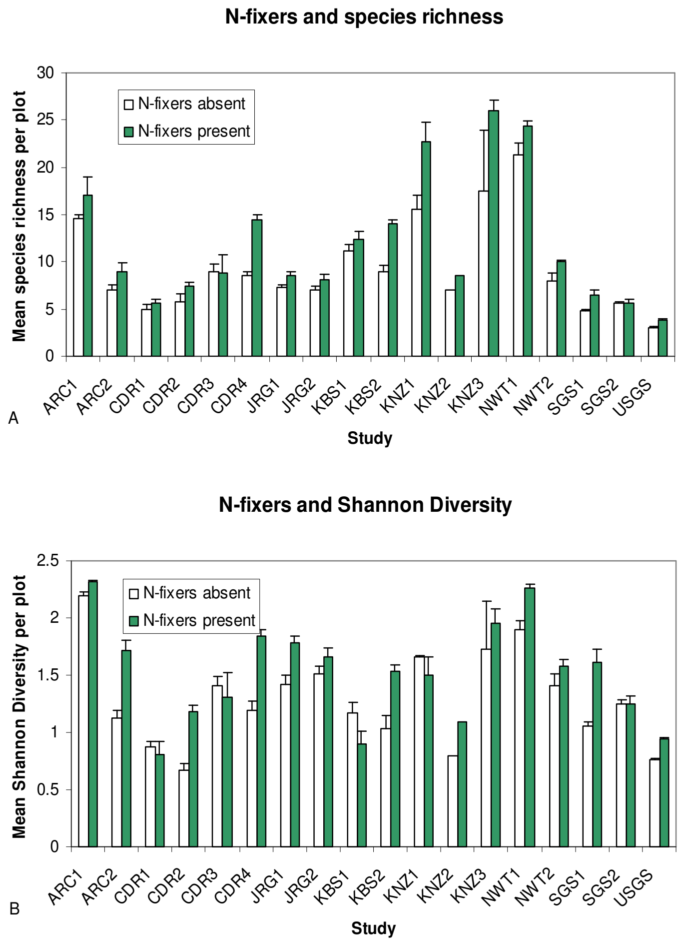

Figure 2. Mean species richness (a) and Shannon-Weiner's Diversity Index (b) as a function of the presence or absence of N-fixers across 17 Fertsyn studies and the USGS study. Plots with N-fixers has significantly higher species richness (paired-t = 3.54, p = 0.0025) & diversity (paired-t = 4.41, p = 0.0004). Study site acronyms: ARC = Arctic LTER, CDR = Cedar Creek Natural History Area LTER, JRG = Jasper Ridge Biological Station, KBS = Kellogg Biological Station LTER, KNZ = Konza Prairie LTER, NWT = Niwot Ridge LTER, SGS = Shortgrass Steppe LTER, USG = USGS dataset. Numbers after repeated acronyms represent unique studies at each site.

Results from both the USGS and Fertsyn datasets indicated that there was a weak inverse relationship between the relative abundance of N-fixers and species richness (Fertsyn: n = 475, $r^2 = 0.03$, $p < 0.001$; USGS: n = 946, $r^2 = 0.04$, $p < 0.001$).

Evenness was better correlated with N-fixer abundance across datasets and the relationship between the two variables was nonlinear (i.e., unimodal or asymptotic) (Fertsyn: n = 475, $r^2 = 0.11$, $p < 0.001$;

USGS: n = 946, $r^2 = 0.32$, $p < 0.001$). For the Fertsyn database, evenness decreased as the relative abundance of N-fixers increased past 30%. For the USGS database, evenness did not appear to decrease even with N-fixer relative abundance near 70%.

Data from 6 of 22 experiments within the Fertsyn database had significant linear relationships between N-fixer relative abundance and that of C3 grasses, C4 grasses, or non-leguminous forbs. The relationships for 5 of the 6 experiments were positive. However, the sample sizes for all but one experiment were small. We thus concluded that additional research is needed to determine the relationship between patterns of N-fixer relative abundance and that of other functional groups.

DISTLM (distance-based multivariate analysis for a linear model) analyses indicated that neither species richness nor N-fixer relative abundance explained much of the variation in plant community composition for the USGS (Fig. 3a) or Fertsyn (Fig. 3b) databases. However, individual study sites included in the Fertsyn database varied in terms of whether N-fixer relative abundance vs. species richness explained more of the variation in the community composition of other functional groups. For example, variation in N fixer relative abundance explained more of the variation in non N-fixer community composition at the Sevilleta LTER. In contrast, variation in species richness explained more of the variation in non N-fixer community composition at Niwot Ridge LTER.

Results of ANCOVAs run using PERMANOVA (permutation-based multivariate anova analysis) indicated that study sites within the Fertsyn database varied a great deal in their species composition (significant site terms in Table 1). The abundance of the focal life form (C3 grass, deciduous woody shrub, evergreen woody shrub, non-leguminous forb, legume, or C4 grass) predicted differences among plots within particular sites (significant site x covariate terms in Table 1). The abundance of

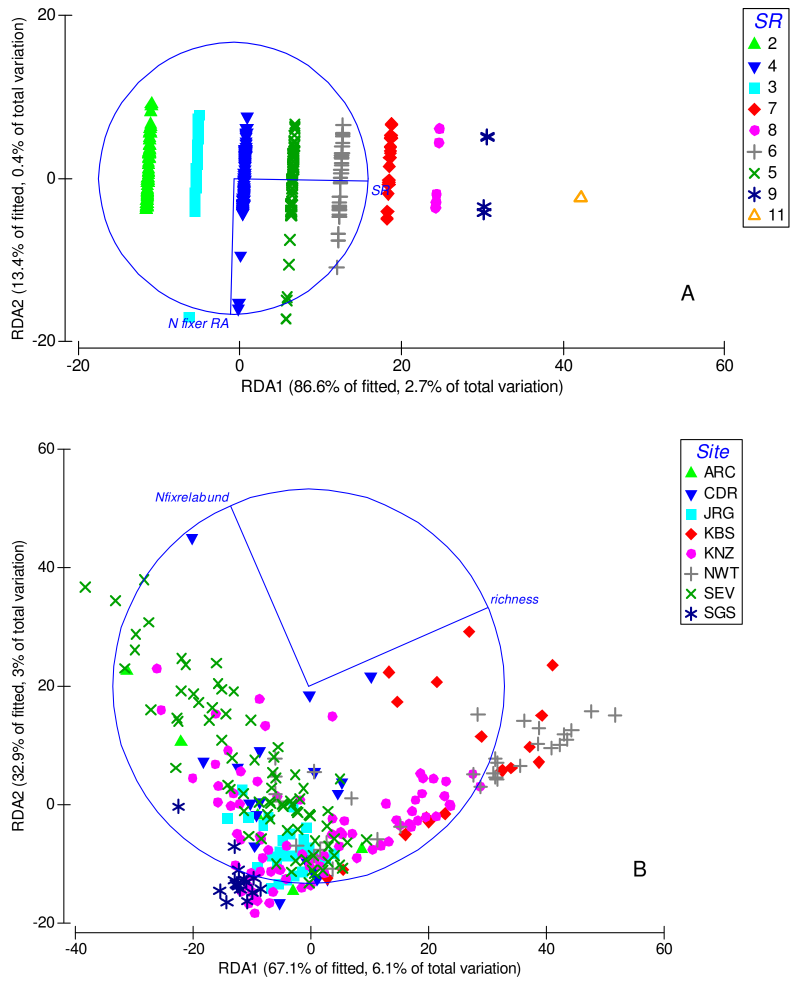

Figure 3. Effects of species richness and N-fixer relative abundance on plant community composition for the USGS (a) and Fertsyn (b) databases. The angles of the lines within each blue circle reflects the degree to which species richness or N-fixer relative abundance correlate with the axes denoted by RDA1 or RDA2. Symbols in each graph represent individual plots included in each database. Colors in (a) denote the species richness (SR) of each plot. Colors in (b) represent different sites. Site acronyms: ARC = Arctic LTER, CDR = Cedar Creek Natural History Area, JRG = Jasper Ridge Biological Station, KBS = Kellogg Biological Station LTER, KNZ = Konza Prairie LTER, NWT = Niwot Ridge LTER, SEV = Sevilleta LTER, SGS = Shortgrass Steppe LTER.

most life forms did not predict differences in the remaining community overall, except for non-leguminous forbs and C4 grasses (both had significant covariate terms in Table 1).

Table 1. Results of PERMANOVA analyses on effect of focal life form relative abundance on remaining plant community composition. Significant results are in bold.

	C3 grass	Deciduous shrub	Evergreen shrub	Forb	Legume	C4 grass
p-value covariate	0.42	0.35	0.57	**0.001**	0.11	**0.045**
p-value site	**0.001**	**0.001**	**0.03**	**0.001**	**0.001**	**0.001**
p-value covariate x site	**0.001**	**0.001**	0.1	**0.001**	**0.001**	**0.001**
# sites	10	7	7	9	8	7
# plots	429	284	277	439	156	377

DELIVERABLES: We are still conducting analyses. Once completed, we will be preparing the following manuscripts for publication:

1. Effects of N-fixers on non-N-fixer diversity and relative abundance in natural communities (Fertsyn and USGS datasets)
2. Temporal trends in N-fixer relative abundance in successional communities and their effects on soil nitrogen availability and species richness (CDR, KBS, Yellowstone datasets)

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