A Functional Approach to Predicting Species Response to N Fertilization across LTER Sites:
A final report of Synthesis Workshops funded by the LTER Network

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Overview. The relationship between aboveground primary productivity, resource fluctuations and species diversity has received considerable experimental and observational attention over the past three decades. In 1996, a group of LTER researchers proposed a working group for NCEAS to bring together data from LTER sites to evaluate the relationship between species richness and productivity across the broad range of habitats included in the LTER Network. This initial synthesis effort (led by R Waide and M Willig) resulted in a number of cross-site synthesis publications (Dodson et al.2000, Schiener et al 2000, Waide et al. 1999, Gross et al. 2000, Gough et al. 2000, Mittelbach et al. 2001[1]). A subset of these initial investigators interested in pursuing analyses of these data to evaluate specific hypotheses related to productivity and diversity in 'low-stature plant communities' has continued cross site synthesis activities over the past decade. The LTER Network Office provided important initial funding for these efforts (three awards, totaling $14,000). This report provides a summary of outcomes of the synthesis activities/workshops funded by the LTER Network. Importantly, the initial investment by the Network for these synthesis activities has seeded funding from other sources (including the LTERs and home institutions of the participating scientists and grants/fellowships from NSF and NCEAS).

Cross-site Activity. Over the past decade, a group from eight LTER sites has participated in a synthesis effort to explore further the wealth of data available from nitrogen fertilization experiments conducted in herbaceous, short-stature plant communities and explore hypotheses related to mechanisms both maintaining and driving changes in species richness and productivity. This group, which has adopted the acronym PDTNet (Productivity-Diversity-Trait Network), includes senior and junior scientists, postdocs and graduate students. Funding from the LTER Network supported five meetings (University of Texas at Arlington in 2002, Sevilleta in 2003, University of Houston in 2004, University of California Irvine in 2005, and NCEAS in 2006) where PDTNet participants met to analyze data, develop hypotheses and outline papers and proposals for continuing these synthesis activities. Additional funding for personnel and analyses were provided by LTER sites of the involved investigators, including supplement requests from NWT (2003) and GCE (2008), and site support for participants to attend workshops and symposia (LTER 2003 ASM and the SEEK data infrastructure project meetings). This level of productivity would not have been possible without additional funding for graduate students and postdoctoral associates that was supported by fellowship funding from NSF to individual participants (e.g. NCEAS Postdoctoral Fellowship to E. Cleland and DDIG to Marko Spasojevic).

Important contributions of this group are summarized below and include graduate training and postdoctoral mentoring in synthesis and analysis, five publications, and, importantly a publically

[1] This paper resulted in an ongoing debate with R Whittaker, recently 'resolved' in a forum in *Ecology* (2010).

accessible synthesis of these data published in *Ecological Archives* (Cleland et al 2008). The dataset includes results from 35 experiments from 10 sites (9 LTER and one other) where resources (primarily nitrogen) were manipulated and responses at the community, species, and ecosystem level measured. We have added to the value of the site level reporting of these data by providing for each species a suite of traits: growth form, life history, relative height, clonality, and origin (native, non-native). In addition, each community type is described according to parameters that may influence functional response: system productivity, species pool, soil characteristics and climatic variables. In the sections below we detail key results of our synthesis activities: I) publications, II) training, and III) data dissemination.

I. Publications. To date, the project has produced 8 publications, including three in *Ecology*, one in *Ecology Letters*, and one in *PNAS*. There are also two manuscripts in advanced stages of preparation and one currently in review. Graduate student authors and co-authors on these papers are indicated by *; postdoctoral associates by ^. The list of publications is provided below; Appendix B includes abstracts of these papers.

2010: Sandel B*, Goldstein LJ*, Kraft NJ*, Okie JG*,Shuldman MI*,Ackerly DD, Cleland EE, Suding KN. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *NEW PHYTOLOGIST* 188: 565-575..

2010: Spasojevic MJ*, Aicher RJ*, Koch GR*, Marquardt ES*, Mirotchnick N*, Troxler TG^, Collins SL. Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits. *ECOLOGY* 91: 1651-1659.

2008: Collins SL, Suding KN, Cleland EE^, Batty M, Pennings SC, Gross KL, Grace JB, Gough L,Fargione JE, Clark CM*. Rank clocks and plant community dynamics. *ECOLOGY* 89: 3534-3541.

2008: Chalcraft DR, Cox SB, Clark CM*; Cleland EE^, Suding KN, Weiher E, Pennington D^. Scale-dependent responses of plant biodiversity to nitrogen enrichment. *ECOLOGY* 89: 2165-2171.

2008: Cleland EE^, Clark CM*, Collins SL, Fargione JE, Gough L, Gross KL, Milchunas DG, Pennings SC, Bowman WD, Burke IC, Lauenroth WK, Robertson GP, Simpson JC*, Tilman D, Suding KN. Species response to nitrogen fertilization in herbaceous plant communities, and associated species trait. *ECOLOGICAL ARCHIVES* E089-070. Ecology 89:1175–1175.

2007: Clark, CM*, Cleland, EE^, Collins, Fargione JE, Gough L, Gross KL, Pennings SC, Suding KN, Grace JB. Environmental and plant community determinants of species loss following nitrogen enrichment. *ECOLOGY LETTERS*10: 596-607.

2005: Pennings, SC, Clark CM*, Cleland EE*, Collins SL, Gough L, Gross KL, Milchunas DG, Suding KN. Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *OIKOS* 110: 547-555.

2005: Suding, KN, Collins SL, Gough L, Clark CM*, Cleland EE*, Gross KL, Milchunas DG, Pennings SC. Functional and abundance based mechanisms explain diversity loss due to nitrogen fertilization. *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES* 102: 4387-4392.

Submitted: Cleland EE, Clark CM^, Collins SL, Fargione JE, Gough L, Gross KL, Pennings SC,

Suding KN. Native and exotic species have different suites of traits: Evidence from a synthesis of nitrogen fertilization experiments. *JOURNAL OF ECOLOGY*: *in review*.

II. Training. The PDTNet has included graduate students and postdoctoral associates since it began in 2003. In addition to participating in workshops, graduate students and postdocs have taken the lead on synthesis products (See above) and 10 students have been co-authors on PDTNet publications. An NSF dissertation improvement grant to M. Spasojevic (UC Irvine) supported the collection of key trait data (SLA) that have now been included in the dataset. In addition, a distributed graduate seminar organized by Cleland, Suding and Collins that involved 44 graduate students at seven institutions through NCEAS focused on analysis of these data (and several publications). Elsa Cleland received a prestigious 3-yr NCEAS Postdoctoral Fellowship to work on this project. Details of these graduate student and postdoctoral training activities are provided in Appendix A.

III. Data Dissemination. The compiled dataset from the PDTNet working group was published *Ecological Archives* (Cleland et al 2008) and provides broad dissemination and use of the data by investigators beyond those familiar with the LTER Network. The productivity, species composition and abundance, and environmental data included in this data set is accessible from individual LTER sites, but this compilation puts all of the data from 35 separate experiments in a common format and contains the standardized measures and functional trait information. The complete dataset and meta-data are available at this link:
http://esapubs.org/archive/ecol/E089/070/default.htm

Appendix A: Graduate student and postdoctoral training activities

1. NSF Dissertation Improvement Grant for graduate student M. Spasojevic. Dissertation research: Predicting community response to nitrogen enrichment using plant traits. P.I. Katharine N. Suding, Co-P.I. Marko J. Spasojevic (PhD student). $15,000.

Abstract. Human activities have increased the amount of available nitrogen globally. This increased nitrogen availability can alter plant communities and lead to diversity loss. One challenge to understanding the impacts of nitrogen enrichment is that communities exhibit a wide range of responses. Why do some communities respond strongly while others do not, and can we identify factors that indicate which communities are most vulnerable? This research will test whether plant traits associated with nitrogen use – specific leaf area, leaf carbon to nitrogen ratios, and leaf nitrogen to phosphorus ratios – can help to understand ecological responses to nitrogen enrichment. It will address two questions: 1) does nitrogen enrichment cause a shift toward species with certain traits, and 2) are there stronger diversity declines in communities composed of species with certain traits and/or with a narrower range of traits prior to enrichment? Encompassing 260 species in 35 nitrogen fertilization experiments in 10 habitats across the United States, the research will quantify relationships among leaf traits and changes in species composition due to nitrogen enrichment.

2. NCEAS Postdoctoral Fellowship for E. Cleland. Shifting plant species composition in response to nutrient enrichment: Can functional traits predict the patterns and rates of change?2005-2008. $220,000.

Abstract. In the course of my post-doctoral research I will seek mechanistic explanations of how nutrient enrichment alters plant community diversity and productivity, by identifying the plant functional traits associated with these changes. I will pay particular attention to species gains and losses, to identify the traits species which invade or become locally extinct, in relation to the initial distribution of functional traits present in the community. In addition, I will ask whether functional traits can predict the rate at which species respond to environmental change. This research will utilize structural equation modeling (SEM), a multivariate statistical technique seldom used in ecology. SEM will be employed in a meta-analytic framework to synthesize many experimental datasets collected from Long-Term Ecological Research sites around the United States, placing this research squarely in the realm of bioinformatics.

3. NCEAS Distributed Graduate Seminar. Ushering in a New Era of Functional Ecology: Dynamics in a Changing Environment. PIs: Suding, Collins, Cleland. Spring semester 2008. $50,000. Involved 44 graduate students from 7 institutions (UCI, UCB, UCSB, UNM, Columbia, U Houston/Rice, FIU).

Abstract. This distributed graduate seminar will engage graduate students in asking fundamental questions about the linkages among environmental change, niche-based functional traits and threshold/divergence dynamics in community structure. Plant functional traits are increasingly being utilized in an effort to generalize species and ecosystem responses to environmental changes, as well as to address fundamental questions in evolutionary ecology. They also present a tool to discern niche or deterministic, convergence, and divergence, and stochastic dynamics in communities. The seminar will focus on emerging areas of research that are advancing functional ecology. Each institution will use datasets that detail community and functional structure from several environmental change manipulative experiments and related observational datasets along environmental gradients. The capstone NCEAS meeting will combine analyses and techniques from each institution to generate predictions regarding national-level responses of plant communities to environmental change such as invasive species and nitrogen enrichment.

Appendix B: Publications and Abstracts

Sandel, B. et al. 2010 *NEW PHYTOLOGIST* 188: 565-575. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation.

Abstract. Patterns of precipitation are likely to change significantly in the coming century, with important but poorly understood consequences for plant communities. Experimental and correlative studies may provide insight into expected changes, but little research has addressed the degree of concordance between these approaches. We synthesized results from four experimental water addition studies with a correlative analysis of community changes across a large natural precipitation gradient in the United States. We investigated whether community composition, summarized with plant functional traits, responded similarly to increasing precipitation among studies and sites. In field experiments, increased precipitation favored species with small seed size, short leaf life span and high leaf nitrogen (N) concentration. However, with increasing precipitation along the natural gradient, community composition shifted towards species with higher mean seed mass, longer leaf life span and lower leaf N concentrations. The differences in temporal and spatial scale of experimental manipulations and natural gradients may explain these contrasting results. Our results highlight the complexity of responses to climate change, and suggest that transient dynamics may not reflect long-term shifts in functional diversity and community composition. We propose a model of community change that incorporates these differences between short- and long-term responses to climate change.

Spasojevic, M.J. et al. 2010. Fire and grazing in a mesictallgrass prairie: impacts on plant species and functional traits. *ECOLOGY* 91: 1651-1659.

Abstract. Fire is a globally distributed disturbance that impacts terrestrial ecosystems and has been proposed to be a global "herbivore." Fire, like herbivory, is a top-down driver that converts organic materials into inorganic products, alters community structure, and acts as an evolutionary agent. Though grazing and fire may have some comparable effects in grasslands, they do not have similar impacts on species composition and community structure. However, the concept of fire as a global herbivore implies that fire and herbivory may have similar effects on plant functional traits. Using 22 years of data from a mesic, native tallgrass prairie with a long evolutionary history of fire and grazing, we tested if trait composition between grazed and burned grassland communities would converge, and if the degree of convergence depended on fire frequency. Additionally, we tested if eliminating fire from frequently burned grasslands would result in a state similar to unburned grasslands, and if adding fire into a previously unburned grassland would cause composition to become more similar to that of frequently burned grasslands. We found that grazing and burning once every four years showed the most convergence in traits, suggesting that these communities operate under similar deterministic assembly rules and that fire and herbivory are similar disturbances to grasslands at the trait-group level of organization. Three years after reversal of the fire treatment we found that fire reversal had different effects depending on treatment. The formerly unburned community that was then burned annually became more similar to the annually burned community in trait composition suggesting that function may be rapidly restored if fire is reintroduced. Conversely, after fire was removed from the annually burned community trait composition developed along a unique trajectory indicating hysteresis, or a time lag for structure and function to return following a change in this disturbance regime. We conclude that functional traits and species-based metrics should be considered when determining and evaluating goals for fire management in mesic grassland ecosystems.

Collins, S.L. et al. 2008. Rank clocks and plant community dynamics. *ECOLOGY*89: 3534-3541.

Abstract. Summarizing complex temporal dynamics in communities is difficult to achieve in a way that yields an intuitive picture of change. Rank clocks and rank abundance statistics provide a graphical and analytical framework for displaying and quantifying community dynamics. We used rank clocks, in which the rank order abundance for each species is

plotted over time in temporal clockwise direction, to display temporal changes in species abundances and richness. We used mean rank shift and proportional species persistence to quantify changes in community structure in long-term data sets from fertilized and control plots in a late successional old field, frequently and infrequently burned tallgrass prairie, and Chihuahuan desert grassland and shrubland communities. Rank clocks showed that relatively constant species richness masks considerable temporal dynamics in relative species abundances. In the old field, fertilized plots initially experienced high mean rank shifts that stabilized rapidly below that of unfertilized plots. Rank shifts were higher in infrequently burned vs. annually burned tallgrass prairie and in desert grassland compared to shrubland vegetation. Proportional persistence showed that and grasslands were more dynamic than mesic grasslands. We conclude that rank clocks and rank abundance statistics provide important insights into community dynamics that are often hidden by traditional univariate approaches.

Chalcraft, D.R. et al. 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. *ECOLOGY* 89: 2165-2171.

Abstract. Experimental studies demonstrating that nitrogen (N) enrichment reduces plant diversity within individual plots have led to the conclusion that anthropogenic N enrichment is a threat to global biodiversity. These conclusions overlook the influence of spatial scale, however, as N enrichment may alter beta diversity (i.e., how similar plots are in their species composition), which would likely alter the degree to which N-induced changes in diversity within localities translate to changes in diversity at larger scales that are relevant to policy and management. Currently, it is unclear how N enrichment affects biodiversity at scales larger than a small plot. We synthesized data from 18 N-enrichment experiments across North America to examine the effects of N enrichment on plant species diversity at three spatial scales: small (within plots), intermediate (among plots), and large (within and among plots). We found that N enrichment reduced plant diversity within plots by an average of 25% (ranging from a reduction of 61% to an increase of 5%) and frequently enhanced beta diversity. The extent to which N enrichment altered b diversity, however, varied substantially among sites (from a 22% increase to an 18% reduction) and was contingent on site productivity. Specifically, N enrichment enhanced beta diversity at low-productivity sites but reduced beta diversity at high-productivity sites. N-induced changes in beta diversity generally reduced the extent of species loss at larger scales to an average of 22% (ranging from a reduction of 54% to an increase of 18%). Our results demonstrate that N enrichment often reduces biodiversity at both local and regional scales, but that a focus on the effects of N enrichment on biodiversity at small spatial scales may often overestimate (and sometimes underestimate) declines in regional biodiversity by failing to recognize the effects of N on beta diversity.

Clark, C.M. et al. 2007. Environmental and plant community determinants of species loss following nitrogen enrichment. *ECOLOGY LETTERS* 10: 596-607.

Abstract. Global energy use and food production have increased nitrogen inputs to ecosystems worldwide, impacting plant community diversity, composition, and function. Previous studies show considerable variation across terrestrial herbaceous ecosystems in the magnitude of species loss following nitrogen (N) enrichment. What controls this variation remains unknown. We present results from 23 N-addition experiments across North

America, representing a range of climatic, soil and plant community properties, to determine conditions that lead to greater diversity decline. Species loss in these communities ranged from 0 to 65% of control richness. Using hierarchical structural equation modelling, we found greater species loss in communities with a lower soil cation exchange capacity, colder regional temperature, and larger production increase following N addition, independent of initial species richness, plant productivity, and the relative abundance of most plant functional groups. Our results indicate sensitivity to N addition is co-determined by environmental conditions and production responsiveness, which overwhelm the effects of initial community structure and composition.

Pennings, S.C. et al. 2005. Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *OIKOS* 110: 547-555.

Abstract. A number of experiments have addressed how increases in nitrogen availability increase the productivity and decrease the diversity of plant communities. We lack, however, a rigorous mechanistic understanding of how changes in abundance of particular species combine to produce changes in community productivity and diversity. Single experiments cannot provide insight into this issue because each species occurs only once per experiment, and each experiment is conducted in only one location; thus, it is impossible from single experiments to determine whether responses of particular species are consistent across environments or dependent on the particular environmental context in which the experiment was conducted. To address this issue, we assembled a dataset of 20 herbaceous species that were each represented in at least 6 different fertilization experiments and tested whether responses were general across experiments. Of the 20 species, one consistently increased in relative abundance and five consistently decreased across replicate experiments. A partially-overlapping group of 8 species displayed responses to nitrogen that varied predictably among experiments as a function of geographic location, neighboring species, or a handful of other community characteristics (ANPP, precipitation, species richness, relative abundance of focal species in control plots, and community composition). Thus, despite modest replication and a limited number of predictor variables, we were able to identify consistent patterns in response of 10 out of 20 species across multiple experiments. We conclude that the responses of individual species to nitrogen addition are often predictable, but that in most cases these responses are functions of the abiotic or biotic environment. Thus, a rigorous understanding of how plant species respond to nitrogen addition will have to consider not only the traits of individual plant species, but also aspects of the communities in which those plants live.

Suding, K.N. et al. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *PNAS* 102: 4387-4392.

Abstract. Human activities have increased N availability dramatically in terrestrial and aquatic ecosystems. Extensive research demonstrates that local plant species diversity generally declines in response to nutrient enrichment, yet the mechanisms for this decline remain unclear. Based on an analysis of >900 species responses from 34 N-fertilization experiments across nine terrestrial ecosystems in North America, we show that both trait-neutral and trait-based mechanisms operate simultaneously to influence diversity loss as production increases. Rare species were often lost because of soil fertilization, randomly with respect to traits. The risk of species loss due to fertilization ranged from >60% for the rarest species to

10% for the most abundant species. Perennials, species with N-fixing symbionts, and those of native origin also experienced increased risk of local extinction after fertilization, regardless of their initial abundance. Whereas abundance was consistently important across all systems, functional mechanisms were often system-dependent. As N availability continues to increase globally, management that focuses on locally susceptible functional groups and generally susceptible rare species will be essential to maintain biodiversity.

Cleland, E.E. et al. 2008. Species response to nitrogen fertilization in herbaceous plant communities, and associated species trait. *Ecological Archives* E089-070. Ecology 89:1175–1175.

Abstract. This synthetic data set contains plant species relative abundance measures from 35 nitrogen (N) fertilization experiments conducted at 10 sites across North America. The data set encompasses the fertilization responses of 575 taxa from 1159 experimental plots. The methodology varied among experiments, in particular with regard to the type and amount of N added, plot size, species composition measure (biomass harvest, pin count, or percent cover), additional experimental manipulations, and experimental duration. At each site, each species has been classified according to a number of easily identified categorical functional traits, including life history, life form, the number of cotyledons, height relative to the canopy, potential for clonal growth, and nativity to the United States. Additional data are available for many sites, indicated by references to publications and web sites. Analyses of these data have shown that N enrichment significantly alters community composition in ways that are predictable on the basis of plant functional traits as well as environmental context. This data set could be used to answer a variety of questions about how plant community composition and structure respond to environmental changes.

Cleland, EE et al. *JOURNAL OF ECOLOGY*: In review.

Summary. 1. Community assembly theories predict that the success of invading species into a new community should be predictable by functional traits. Environmental filters could constrain the potential pool of successful ecological strategies in a given habitat, such that native and successfully invading exotic species will have similar suites of traits (convergence). Conversely, concepts of limiting similarity and competitive exclusion predict that native species will prevent invasion by functionally similar exotic species, resulting in trait divergence between the two species pools. Nutrient availability may further alter the strength of convergent or divergent forces in community assembly, by relaxing environmental constraints and/or competitive interactions.
2. To investigate how nutrient availability influences forces of divergence and convergence during the invasion of exotic species into native communities, we conducted multivariate analyses of community composition and functional traits from naturally assembled plant communities in long-term nitrogen (N) addition experiments from across North America.
3. The relative abundances of key functional traits differed between the native and exotic plant communities, consistent with limiting similarity or a trait bias in the exotic species pool. Environmental context also played an important role in invasion, because sites varied in the identity of the traits that predicted dissimilarity between native and exotic communities. Nitrogen enrichment did not alter these patterns.
4. Nitrogen enrichment tended to increase exotic abundance, but this result was driven by a dramatic increase in exotics in only a few experiments. When similarity between native and exotic communities was included in the statistical model, N enrichment no longer predicted

an increase in exotic relative abundance. Instead sites with the highest abundance of exotic species were the ones where native and exotic communities had the highest trait similarity.
5. Synthesis: Our analysis of natural patterns of invasion across herbaceous communities in NorthAmerica found evidence to support both divergent and convergent forces on community assembly with exotic species. Together these results suggest that while functionally dissimilar exotic species may be more likely to invade, they are unlikely to become abundant unless they have traits that pre-adapt them to the environmental conditions in their invaded range.