Papers in process as of the 2010 NutNet workshop (Aug. 2010)

Productivity and diversity

Getting over the hump – the last productivity-diversity paper?
Lead contact: Peter Adler et al; **opt-out paper**
Productivity and species richness has been a popular topic for at least three decades. Because of early evidence of a simple relationship between diversity and productivity, this relationship began to be used to infer local ecological processes from easily collected data. However, because variation in methods (e.g. no standard methods across studies, no direct measurements of productivity, simplistic view of causality) led to a multiplicity of patterns and interpretations of the relationship between productivity and diversity, considerable confusion arose. A variety of reviews and meta-analyses in the past decade have examined this relationship; however the continued variation in the results suggests that directly comparable sampling across a wide range of productivity is still required for a truly synthetic understanding of these relationships. Here we use a standard sampling protocol to quantify this relationship within and across 50 grassland sites on 5 continents, encompassing a wide diversity of rainfall, precipitation, and vegetation types. While some sites show evidence of the original simple relationships between productivity and diversity, we find no support for a general within-site relationship between these factors. Globally, there is some evidence for limitation of species richness in unproductive sites, but this relationship provides little explanatory power. Thus, even with standardized methods generating directly comparable data, the lack of a strong within or among-site relationship between productivity and richness in the current study strongly highlights the need for more sophisticated approaches for understanding how resource availability influences species richness.

A global test of whether niche complexity begets diversity
Lead contact: Stan Harpole
The search for a general understanding of the processes underlying coexistence of similar species lies at the core of most of the field of community ecology. One of the most general theoretical predictions is that varying resource ratios can lead to high-dimensional niche space that can allow the coexistence of numerous potential competitors. This theoretical prediction has withstood strong tests at a few sites, suggesting the intriguing possibility that there may be a general law governing species coexistence in complex communities. Here we report the results of a test of this theory at 50 grassland sites in seven countries using a coordinated network of observational studies and nutrient-addition experiments. Here we find that approximately one species is lost for each nutrient added, suggesting that nutrient diversity and multiple limitation can act to maintain biodiversity. The results of this work have strong implications for our search for general laws underlying community ecology and suggest that human alterations of global nutrient cycles may drive significant species extinctions.

Light mediation of the diversity-productivity relationship in grasslands
Lead contact: Yann Hautier (2009 paper)
Abstract: Humans have greatly enhanced the rate of supply of nutrients worldwide. In many types of ecosystem this eutrophication causes loss of plant species diversity. Fertilization increase productivity and canopy height and lead to reduced light in the understory. In grasslands, an increase in competition for light has been shown to be a major mechanism of this plant diversity loss while competition for nutrients played no detectable role. Here, we use structural equations models to examine the relative importance of competition for light versus competition for nutrients as driver of diversity–productivity relationships using a network of XX sites from grasslands around the world manipulating three key nutrients (N, P, K).

Nutrient limitation and grassland productivity

What limits productivity in grasslands worldwide?

Lead contact: Jean Knops, **opt-out paper**

Uniformly-collected datasets to evaluate the importance of different soil nutrients for limiting grassland productivity at the global scale are lacking. We analysed data from a nutrient-addition experiment conducted at xx40 grassland sites across five continents to describe patterns of N, P, K and micronutrient limitation in relation to total above-ground biomass. Based on other analyses in terrestrial ecosystems we hypothesized that nitrogen is a significant limit at most sites, phosphorus limitation is more prominent on old, weathered soils, and that limitation or co-limitation by other nutrients may also occur. We investigated how the extent and nature of nutrient limitation varies with continent, latitude and climatic parameters. Consistent with expectation, nitrogen was a strong nutrient-related limit to above-ground biomass ... Effects of P were dependent on... and there were strong interactions between site, N, P and K... Effects were mediated by …...

Do nutrients other than N and P matter for grassland biomass?

Lead contact: Stan Harpole

Limitation by elemental nutrients represents one of the major and general constraints on autotrophic production. While synergistic co-limitation of plant biomass by phosphorus (P) and nitrogen (N) is globally widespread in natural systems, comparatively little is known about the general patterns of limitation by other macro and micro nutrients, especially in the context of N and P co-limitation. Here we show, first, using meta-analysis of XXX fertilization studies that manipulated combinations of P, N and other nutrients that nutrients other than N and P appear to be generally limiting to plant biomass across terrestrial, marine and freshwater systems. Furthermore, fertilization by "other" nutrients, in combination with N and P, led to synergistic increases in biomass. Motivated by our meta-analytic results, we performed a "meta-experiment" to test the hypothesis of limitation by nutrients other than N and P, focusing specifically on XX identically implemented and sampled experimental sites in terrestrial grassland systems across five continents. We found that, on average, terrestrial grasslands were... We conclude that because of the enormous increases in N and P cycling due to human activities, ecosystems may likely experience progressively greater limitation by other resources.

Decomposition

Drivers of aboveground primary production and litter flux in grass-dominated ecosystems

Lead contact: Lydia O'Halloran (2009 paper)

Abstract: Predicting ecosystem feedbacks to global carbon cycling in response to impending climate change requires an understanding of both spatial and temporal patterns of ecosystem carbon fluxes as they vary with temperature and precipitation. Grasslands are ideal systems for quantifying the pools that contribute to these fluxes because they occupy diverse biogeographic regions throughout the world and experience a range of abiotic conditions that are likely to control regional-scale patterns in biodiversity and primary production. Here, we explore the relationship between the climatic characteristics of mean annual precipitation, interannual variability in precipitation, and mean seasonal temperature and ecosystem traits including aboveground primary production, litter accumulation and litter loss rates using data from 42 grassland sites following a common protocol.

Our results suggest that although all of the sites are grass-dominated, the variables controlling major ecosystem functions, such as aboveground primary production and litter accumulation, differ profoundly among sites. In contrast to grassland production paradigms, neither precipitation nor latitude appear to be driving ecosystem functions in these grasslands suggesting precious paradigms may hold for within site relationships year to year but at landscape or global scales. This global scale study demonstrates the importance of within-biome variation in response to abiotic conditions, highlights the need for incorporation of this variability into existing dynamic global vegetation models, and provides validation data for such models.

Global variation in nutrient limitation of grassland litter decomposition.
Lead contact: Sarah Hobbie
Abstract: We aim to use a global cross-site study of nutrient limitation in grassland ecosystems to explore how the effects of nitrogen (N), phosphorus (P), and micronutrients (K) change depending on geographic location. We will use data on live and dead biomass to calculate single exponential decay constants (assuming steady state conditions), and compare them in a factorial N x P x K experiment at grassland sites, worldwide. We will test the following hypotheses: that (1) N will limit decomposition at younger, less weathered sites (e.g., in North American and European sites and at higher latitudes), while P or micronutrients will limit decomposition at older sites (e.g. in Australia and at lower latitudes), (2) nutrients (either N, P, K) will limit decomposition more strongly in wetter sites than drier sites, (3) nutrients will have greater effects on decomposition in those sites where nutrient addition has led to greater abundance of PFTs that are yummy (legumes, forbs) compared to PFTs that are not yummy (C4 grasses), and (4) nutrient effects will become stronger through time because of species compositional changes that will reinforce nutrient effects.

Species turnover

Drivers of spatio-temporal variation in the composition of globally distributed herbaceous communities
Lead contact: Peter Wragg
Terrestrial plant community composition varies across time and space on landscapes. Understanding of the patterns and drivers of this turnover is essential for understanding patterns (e.g. gradients) of diversity and their covariation with spatial and temporal scale. We will use NutNet's extensive and consistent sampling scheme to describe patterns of variation through space and time in the species, phylogenetic, and trait composition of communities. We will examine variation through space using the nested experimental structure (plots within blocks within sites) as well as the decay of similarity with distance between plots (plot co-ordinates to be obtained from site investigators). The first few years of data from the control plots will provide information on rates of turnover through time. We will explain variation in these turnover patterns using plot-, block-, and site-level variables such as productivity, environmental heterogeneity, climate, and species pool size. Given the inherent scale-dependence of diversity, the uniquely standardized sampling scheme of NutNet should yield robust new insights into global patterns and correlates of compositional turnover. For example, we will contribute to the debate on the form and causes of the relationship between turnover and productivity, a key factor in the scale-dependent diversity-productivity relationship. This analysis will provide a context for interpreting the effects of the treatments on compositional turnover.

Nutrients and functional group responses

Resource driven compositional shifts in grassland communities: nutrients, functional groups, and traits

Lead contact: Elsa Cleland

Nutrient availability may alter patterns of total biomass differently than the component parts of a local community. For example, the relative cover and biomass of plants, grouped by function (e.g. legume, forb, grass) or traits (e.g. photosynthetic pathway, provenance), may change substantially but the aggregate community biomass may be constrained by site level nutrients or precipitation, thus remaining more constant. Here we examine the relative importance of resource identity, resource supply rates, and resource ratios on the cover and biomass of plants grouped by function and traits. Using identical experimental methods in 50 grassland sites on 5 continents, we examine the generality of changes in functional group relative abundance and aboveground biomass production to a factorial combination of N, P, and K. We find that, across the extreme diversity in abiotic conditions represented in this study, the cover of legumes declines with N addition but increase in treatments in which K and micronutrients are added. In contrast, forb cover increases with added N, but declines with addition of K and micronutrients. Grasses have no consistent response to nutrient identity or resource supply ratios. Legume biomass increases with P and some factorial combinations of N, P, and K. We'll eventually look at photosynthetic pathway and provenance and tell you the answer when we complete this analysis. Clearly biomass and cover are driven by differential responses to nutrients.

Plant invasions

Abundance at home is a good predictor of abundance away for introduced plants

Lead contact: Jennifer Firn (2009 paper)

Few studies have explicitly addressed the assumption that plant species are more abundant in their introduced ranges. Given the prevalence of human disturbance globally, an alternative scenario is that abundance patterns in home and away habitats will be matched because disturbance-tolerant dominant species should thrive. Tests are limited to a few highly invasive species with known rarity at home, and may thus be biased. In this global-scale study, we evaluated this 'abundance' assumption using data for 26 grassland plants from 42 locations in eight countries, and included home and away sites for each species. The species [14 grass, 12 forbs] were selected randomly with respect to their home abundances. We found grass species that were abundant in their home range were similarly abundant in their invasive range. Forb species were significantly more abundant at sites in their home range, but abundance at sites in the native and invasive range were still positively correlated. Extending this analysis to the community level by pooling our species, we found similar composition and abundance hierarchies at sites in different countries, when more than six species were included in the communities. This suggests that as disturbance regimes are introduced in the away ranges, invading communities assemble similarly as they do at home as long as the species pools match. As such, our findings show that the abundance of plant species at native sites should be an important consideration in biosecurity screening procedures.

Native-exotic richness relationships in the world's grasslands -- biogeography drives local-scale correlations

Lead contact: Andrew MacDougall

While experiments at single sites have demonstrated that diverse communities can be less invasible, larger scale studies of this question are based primarily on examining the correlation between native and exotic richness. A general finding of this work has been a negative correlation between native and exotic richness at small spatial scales. However, this approach is subject to a major confounding of potential causation -- are rich sites more resistant to invasion are does invasion cause native extinction? Leaving causation aside, the suggestion that native diversity can mediate invasion suggests a link between the large-scale drivers of diversity and patterns of invasion. One of the most studied and debated relationships in ecology is the effect of productivity on community diversity. The shared variable, native richness, suggests a link between the bivariate diversity-productivity and native-exotic richness relationships. However, the links between these two well-known relationships remain largely unexplored. Here we review and synthesize the links between the diversity-productivity and native-exotic richness literature to generate testable linkages between the abiotic environment, community richness, and exotic richness. We then test these relationships using a unique set of community composition data collected at XX grasslands sites in nine countries. In addition to increasing our understanding of invasion processes, this work demonstrates the power of potentially transformational scientific approach that bridges the gap between locally replicated experimental work and meta-analyses that has relevance to many areas of ecology.

Biological invasion in the world's grasslands

Lead contact: Eric Seabloom (2009 paper) **opt-out paper**

Biological invasions are one of the major threats to global biodiversity and impose huge financial costs on human society due to loss of crops, damage to infrastructure, and changes in basic ecosystem processes such as fire regimes, hydrology, and nutrient cycling. In addition, biological invasions have much to teach us about basic ecology and evolution. While many local-scale experiments have provided insight into basic mechanisms governing the probability of invasion and its impacts, larger scale studies rely on observational data and meta-analyses. While insightful, these synthetic works are limited by the need to use heterogeneous data that is typically observational. Here we present the results of a global scale study and experiment examining the patterns and drivers of biological invasions in the world's grasslands. Grasslands cover 40% of the earth's land surface and are the most critically endangered terrestrial biome. Conversely, grasses are some of the most invasive of all species. Here we compare the richness of and dominance of exotic species in XX grasslands in nine countries that include salt marshes, mesic prairies, savannah, and alpine tundra. We subjected YY of these systems to factorial combinations of nutrient addition and herbivore exclusion, two forces commonly invoked to explain exotic dominance. Although, most experimental work focuses on the role of local processes in mediating grassland invasion, we found that biogeography dominates the number and impacts of exotic species. More than 80% of the variability in exotic richness and dominance arises from differences between habitats and among sites within habitat types. We found that fertilization led to an increase/decrease in exotic species. The presence of consumers also had strong/weak positive/negative effects on invasion. We also found a strongly bimodal pattern in the distribution of exotic cover in which nearly all sites were either largely pristine or nearly completely dominated by exotic species. The lack of sites with an equitable mixture of native and exotics is suggestive of positive feedbacks leading to two alternate states.

Are naturalised plants doing something different than natives?

Lead contact: Jennifer Firn

Darwin proposed that naturalized plant species are less likely to coexist with native congeners because similarities between these species result in competition for niche space, and limitation by herbivores and pathogen attack. This theory suggests that introduced species are doing something 'different' to the native species they coexist with in their new range, although evidence is mixed. We use the results from a global meta-study, the Nutrient Network, to explore whether introduced species are different to native flora. To do this we compare the abundance of native and introduced congeners across regional and local scales. We then also investigate the general pattern and importance of functional group similarity (e.g. life-history and photosynthetic pathway). The extensive number of sites in the network will allow us to test the generality of Darwin's Naturalisation Hypothesis and the struggle for existence.

How do fluctuating resource conditions alter the abundance of introduced species home and away?

Lead contact: Jennifer firn

Disturbance is identified as a key driver of the dominance of plant species in their introduced range. Increases in resource conditions are a common disturbance found to promote the dominance of introduced species as described by the Resource fluctuation hypothesis. To date, this hypothesis has been used to understand how the conditions of a habitat and propagule pressure facilitate the success of an introduced species in a new range. Few studies have explored whether the abundance of a given species is also facilitated by the same disturbance at sites in their native range. If this is indeed the case than tolerance to disturbance could also be described as a species trait and therefore be used to describe the invasive characteristics of a species. In a global meta-study called the Nutrient Network, we test the response of 26 species [11 grasses and 10 forbs] to nutrient fluctuations (nitrogen, phosphorous, potassium and micronutrients) at 33 sites in both their native and introduced range. This is the first study to test the response of multiple introduced species (invasives and non-invasives), at multiple sites home and away to the same magnitude of nutrient increase. These results are key for understanding how resource availability at a site and the traits of a species drive a change in community composition to promote invasion and whether these characteristics hold for species home and away.