**Slide 1:**

* Nitrogen enrichment is a major threat to biodiversity worldwide. Changes to biogeochemical cycling through atmospheric deposition, fertilizer runoff, and land use change are implicated in the ongoing global biodiversity crisis.
* The nitrogen enrichment effect has been well studied. Classic frameworks to understanding the pathway of N-driven diversity loss suggest that N enrichment increases plant productivity, reducing the number of light sensitive species and presenting fewer opportunities coexistence.
* N enrichment may also reduce spatial heterogeneity in limiting resources, reducing the number of opportunities for spatial coexistence.

**Slide 2:**

* However, much of our understanding of how nitrogen enrichment impacts plant diversity comes from relatively small-scale experiments that evaluate change in a limited spatial context, often 1m2 or less.
* Concerns of scale are persistent in ecology, and recent scholarship has suggested that the impacts of human-induced environmental changes may depend on the extent of sampling. Effects may stay constant, change in magnitude, or even invert depending on the scale sampled.
* Evaluating these scale dependent relationships can give nuanced insights into the mechanisms of N-driven biodiversity change, particularly related to changes in species richness, abundance, and spatial pattern.

**Slide 4:**

* As an example, say we have a community that contains 6 species. In response to an experimental treatment, the overall community diversity is reduced. In addition, the community becomes more homogenized spatially.
* Borrowing much from a framework for analysis presented by the MOBR package.

**Slide 5:**

* The simplest way we can understand this change is to compare diversity as a function of familiar alpha, beta, and gamma diversity relationships.
* In this case, we see that our experimental treatment increased alpha-level diversity very slightly in community 2, but resulted in a large decrease in the total diversity found in the sampling area.
* As a result, we may also conclude that turnover (beta - the relationship between alpha and gamma diversity) is reduced in response to treatment.

**Slide 6:**

* This sort of analysis only gives us information on two coarse scales, however.
* More nuanced information can come from further decomposition of these relationships into their individual sample-based rarefaction curves, which can demonstrate how exactly diversity effects change with scale, and how spatial patterns may be influencing these patterns..
* There are two methods of constructing sample-based rarefaction curves, in which observed diversity is determined as a function of sampling effort.
  + Spatially, in which the next unit of sampling effort is the closest, spatially, to the point of origin. In this case, we find that that the control community accumulates species much more rapidly than the nutrient added one, with a key threshold of around 10 samples needed before it overtakes the nitrogen added curve.
* To assess the changes in spatial pattern that may accompany nutrient enrichment, we may use the same rarefaction method as before, though this time accumulating samples at random. If diversity in a community is more spatially aggregated than another, we will find that it will encounter new species more rapidly in this random structure.
* Comparing the observed differences between curves in the random and spatial rarefaction cases can give us a sense of how spatial aggregation structures spatial pattern in communities. In this case, our control community is more spatially structured that our nutrient community.
* While shown here using just species richness, effective number of species metrics, which account for abundance-weighted diversity change can be used in a similar fashion.

**Slide 7:**

* California grasslands are an ideal system within which to examine the drivers of scale-dependent relationships in response to nitrogen enrichment.
* Highly spatially heterogenous, California grasslands exhibit very high diversity despite their exotic diversity – 10 or more species per square meter.
* Current understanding often suggests that fertilization enhances the growth of exotic grasses at the expense of native forb and legume species.

**Slide 8:**

* Using this framework, we asked several key questions:
* 1. How do choices of sampling scale affect our interpretation of nitrogen-driven biodiversity change?
* 2. To what degree is the scale-effect relationship dependent on changes in species richness and relative abundance?
* 3. How do changes to community spatial patterns affect our interpretation of scale-dependent effects?

**Slide 9:**

* To assess scale-dependent patterns of nitrogen enrichment effect on plant diversity, we established a nested plot experiment at three University of California reserves.
* In each reserve we established 4 blocks, each consisting of 2 paired plots
* Each subplot was then divided into an 8x8 grid containing .5m x .5m subplots spaced every 1m.
* We then randomly assigned one plot out of each pair to an experimental fertilization treatment, consisting of a slow-release urea fertilizer applied at a rate of 10g N/m2 in winter months.

**Slide 10:**

* To assess key responses to N-driven biodiversity change, we collected data on three response variables.
* The first, community diversity and percent areal cover, was collected in all subplots at three times in each year, corresponding to peak phenological periods to ensure that all representative species were sampled.
* Light was measured using a 10-cell PAR sensor placed above and below the grass canopy in 10 random locations within each plot.
* We also measured changes in plant productivity using clipped strips of aboveground biomass in the margins between individual subplots.

**Slide 11:**

* Consistent with prior studies of nutrient enrichment, nitrogen addition produced significant increases the amount of light interception in both years, indicating an increased demand for light as a limiting resource.

**Slide 11:**

* Commensurate with an increase in light limitation is an increase in plant productivity, though it appears these measures were more variable and did not result in statistical significance for either year.
  + Need to double-check

**Slide 12:**

* Despite this increase in light limitation, permutation-based tests of significance indicate that communities showed no significant change in either species richness, or abundance-weighted diversity. This is not surprising – California grasslands, as an annual system, are likely to take more than one year for nutrient enrichment to affect community assembly.

**Slide 13:**

* After two years of treatment, however, nutrient enrichment shows marked effects, though interpretation differs significantly depending on the choice of metric used.
  + When purely focused on species richness, comparison of alpha-beta-gamma relationships indicate that nitrogen enrichment results in a substantial decline in alpha-scale diversity, though did not appear to cause consistent reductions in the total number of species present within the entire spatial extent of sampling. This change corresponds with an interpreted increase in beta diversity – the turnover in species richness found within subsamples in each plot.
  + Incorporating abundance-weighted metrics into analysis, on the other hand, demonstrates declines in diversity that are consistent at both the individual sampling unit and whole plot scale, with no significant change in the turnover of these communities.

**Slide 14:**

* Further decomposition of species richness change into its constituent accumulation curves indicates that response change with sampling effort was highly nonlinear – even small increases in sample accumulation dramatically reduced effects of nutrient enrichment.
* When this spatial accumulation curve is compared to its random counterpart, we see a greater observed magnitude of diversity change when reducing the influence of spatial structure. This change suggests that our control communities exhibit a somewhat higher degree of spatial aggregation (clumping) at small sampling scales.

**Slide 15:**

* Use of abundance-weighted metrics to calculate diversity change effects indicates a far more linear response as a function of sampling effort – regardless of the number of samples taken, nutrient enrichment effects on the relative abundances of different species appears roughly consistent.
* Moreover, the spatial aggregation effect in control treatments is far more pronounced when incorporating abundance into estimates of diversity change, and is detectable at far greater sampling efforts.

**Slide 16:**

* Together, these results show a set of key findings-
  + Effects of nutrient enrichment do vary considerably with sampling scale – provided that species richness is your response!
  + It seems that nutrient enrichment is unlikely to cause species extirpations, even at relatively small scales, simply due to increases in sampling effort can reach similar asymptotes of species richness.
  + However, abundance-weighted metrics show remarkably consistent effects across scales.
  + Changes in spatial distribution are an important part of nutrient enrichment, that may change the way communities operate, independent of diversity loss!
    - Storage effects
    - Response to disturbance
    - Dispersal

**Slide 17:**

* Acknowledgements:
  + **Plant Sciences, etc.**
  + **Any specific funding sources that must be attached to all things that go out of the lab?**