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Resource heterogeneity does not explain the diversity-productivity relationship across a boreal island fertility gradient

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Many studies at the regional scale have found either negative or hump-shaped relationships between productivity and diversity, and some theories propose that these occur because soil resource heterogeneity is either lower or less important in more productive environments. However, there have been few explicit tests of these theories in natural ecosystems. We evaluated the relationship between soil resource heterogeneity and plant richness within a well characterized system of 30 islands in northern Sweden across which soil fertility and productivity declines, and species richness increases, as a consequence of ecosystem retrogression. On each island we created a spatially explicit grid consisting of 49 sampling points in a 9.5 m quadrat, which we used to quantify spatial heterogeneity of five soil variables (NH_4^+-N, amino N, PO_4^--P, microbial biomass, and decomposition), and plant community composition. Using a hierarchical Bayesian approach, we estimated mean semivariograms of each variable for each island size class to compare three components of spatial heterogeneity: total variability, spatial grain, and patchiness. This analysis showed that variability within islands was usually lowest on small islands, where species richness was highest and productivity lowest; however, NH_4^+-N and amino N had greater patchiness and spatial grain on small islands. We did not detect any significant across-island correlations between whole-plot plant species richness and either whole-plot standard deviation or coefficient of variation of any soil variable. Using partial Mantel tests, we found that mean correlation coefficients between within-plot plant community composition and the soil variables were never significant for any island size class, and did not differ between island size classes. Our findings do not provide any evidence that soil resource heterogeneity controls the productivity-diversity relationship in this system, and suggests other mechanisms are primarily responsible.

A central focus in ecology is to understand the underlying mechanisms that generate and maintain patterns of species diversity. One factor that is often considered to be of importance in determining plant species diversity is the heterogeneity of limiting resources (Hutchinson 1959, Tilman 1982, Tilman and Pacala 1993, Huston and DeAngelis 1994). The resource heterogeneity hypothesis (RHH) proposes that for a given area, increasing resource heterogeneity increases the number of species that can coexist, resulting in higher species diversity (Hutchinson 1959, Ricklefs 1977, Tilman 1982, Tilman and Pacala 1993, Mittelbach et al. 2001). This is proposed to occur because plant community members have different resource niches that allow each species to be competitively dominant under a different combination of local resource conditions (e.g. MacArthur and Levins 1967, Ricklefs 1977, Reynolds et al. 2007). Therefore, according to the RHH, areas with variable resource conditions will result in patch-scale dominance of different species, and will therefore result in higher diversity relative to areas with spatially homogeneous resource conditions (Tilman and Pacala 1993).

The general premise of the RHH has been incorporated into several theories that aim to explain the relationships between diversity and productivity (Tilman and Pacala 1993, Huston and DeAngelis 1994, Abrams 1995). Productivity-diversity relationships are often observed to be negative or hump-shaped (Ricklefs 1977, Tilman and Pacala 1993, Grace 1999, Mittelbach et al. 2001), and the underlying mechanisms that control this pattern have been the subject of substantial debate (Abrams 1995, Waide et al. 1999, Craine 2005). Several models have proposed that decreasing diversity at high levels of productivity occurs because of a decrease in soil resource heterogeneity as productivity increases (Tilman 1982, Tilman 1987, Abrams 1988). Other diversity models have suggested that diversity decreases at high levels of productivity because there is a